FOOD RESOURCE USE AND RESPONSES TO CHANGES IN PREY AVAILABILITY OF COMMON AND THICK-BILLED MURRES (Uria aalge and U. lomvia) BREEDING AT THE GANNET ISLANDS, LABRADOR

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by

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The company of these birds in the field is guileless.

It is easy to feel transcendent when camped among them.

- *Barry Lopez, 1989,* Arctic Dreams

ABSTRACT

This work focused on two sets of comparisons: the first was an inter year comparison of the chick diets and related breeding parameters of Common and Thick-billed Murres (*Uria aalge and U. lomvia*) breeding at the Gannet Islands, Labrador before and after a local decline in capelin abundance. The second was an interspecies comparison of these parameters. In 1996 and 1997, years of locally low capelin abundance, I measured murre chick diet composition , feeding rates, breeding success, chick growth, adult masses, maximum dive depths and off-duty pair members' time spent at site. I then compared these data with those gathered by previous researchers in years when capelin were more abundant (1981, 1982 and 1983). After the decline, murres fed their chicks up to 75 per cent less capelin and up to 65 per cent more daubed shannies than they had fifteen years previously. Feeding rates of both species varied by up to 250 per cent among the five years, but this variation was not concomitant with changes in the proportion of capelin in the chicks' diets. The murres' dietary shift did not seem to affect their colony attendance adversely; counts of both murres on some plots increased, while on others they did not differ significantly. Neither murre species had significantly different breeding success among years. Chicks of both species grew well following the decline in capelin availability. Masses of adult murres were not significantly different after capelin became scarce. No time-at-site data were taken before the decline in capelin abundance, but after the decline, members of chick rearing Common and Thick-billed Murre pairs both spent a mean of ten minutes together at their sites per feeding visit. Results from the interspecies comparison suggest that chick food resource partitioning might have been negligible between Common and Thick-billed Murres at the Gannet Islands in 1996 and 1997. In both years, the murres' chick rearing periods overlapped almost exactly. In the year they were both measured, the sizes of the principal item in their chicks' diets did not differ

significantly. During one of two all- day feeding watches, the murres' chick feeding peaks were concurrent, but during the other they were not. In the year dive depths of both species were measured, Common and Thick-billed Murres dove to similar maximum depths.

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made assiduous arrangements to ready the Gannet Islands field camp for its first season after 13 years of disuse. James Williams lent his time and his ideas to making dive-measuring devices. Roy Ficken, Ed Oliver and Pat Squires came to the rescue more times than I can count by developing slides, ordering equipment and keeping track of administrative matters.

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CHAPTER 1

GENERAL INTRODUCTION

If ecosystems are like symphonies, populations are like notes of music. A stock of capelin, for instance, could be imagined as the utterance of a flute. The krill on which they feed might be the resonant sound of a cello. We could even conceive of the capelin's seabird predators as a French horn's sonorous note. As one season courses into the next, notes string themselves like beads along a melody's thread. Because no population exists in isolation, one's tune constantly interweaves with those of its predators and prey, parasites and symbionts. In this way, single melodies combine to form harmonies, and harmonies unfurl into symphonies.

Extending this analogy, describing one aspect of a population's biology - diet composition, for instance - can be likened to describing a chord in the symphony of its ecosystem. The identification of such chords is interesting and important. However, more informative investigations aim to transcribe a greater portion of the ecological opus. For example, they might inquire into how a population's diet corresponded with breeding parameters or behaviours, or with other species' abundances and distributions. Moreover, an informative inquiry might assess, among other things, how that population's feeding ecology converged on or diverged from another's.

With this study, I describe Common and Thick-billed Murre (*Uria aalge* and *U. lomvia)* chick diets at the Gannet Islands, Labrador in 1996 and 1997. In doing this, I identify single chords in the symphony of the murres' ecology. Delving into the more complex dynamics of its music, I also attempt to clarify the relationships between the murres' chick diets, prey abundance and breeding parameters, as well as ascertain the extent to which breeding Common and Thick-billed Murres share or partition their food resources.

I conducted this study at the Gannet Islands Ecological Reserve (53 57' N, 56 31' W) (Figure 1.1). Seven small islands huddled together against the tantrums of the Labrador Sea, the Gannet Islands occupy a fortuitous location. They lie directly in the path of the Labrador Current, and are about 60 kilometers west of Hamilton Bank. The Labrador Current carries cold polar water south, facilitating the upwelling of nutrients on which plankton thrive. Productivity depends not only on nutrients, but on sunlight as well. So the productivity associated with the Labrador current is amplified in shallow areas where light penetrates most of the water column. For instance, the light-drenched waters over Hamilton Bank, as well as those along the nearby Labrador coast have historically supported especially high concentrations of marine life, from phytoplankton to blue whales. The Gannet Islands are thus located near some of the most highly productive waters in the northern hemisphere during the summer (Ocean Color from Space: Global Seasonal Change, 1998).

Students of colonial seabirds generally agree that uncommonly high concentrations of prey in part determine the birds' choice of colony locations (Lack, 1954; Horn, 1968). The Gannet Islands' location in the highly-productive southern Labrador Sea might in part explain the great abundance and diversity of breeding seabirds there. In fact, the islands are home to Labrador's most diverse alcid colony. Approximately 50,000 pairs of Common Murres and 6,000 pairs of Thick-billed Murres converge on the islands to breed each summer. In addition to murres, an estimated 6,400 pairs of Razorbills (*Alca torda*), 39,000 pairs of Atlantic Puffins (*Fratercula arctica*) and 110 Black Guillemots (*Cepphus grylle*) mate and raise their young each year at the Gannet Islands (Lock *et al.*, 1994).

Near the southern extent of the Thick-billeds' range and the northern extent of the Common Murres', the Gannet Islands Ecological Reserve is one of the only places in the western Atlantic where the murres breed syntopically and in high numbers. The rare co-

occurance of both murre species, combined with high auk diversity renders the Gannet Islands an ideal place to conduct seabird research. Consequently, in 1981, 1982 and 1983, T.R. Birkhead led a group of Canadian Wildlife Service (CWS) researchers to study the breeding biology of alcids at the Gannet Islands (Birkhead and Nettleship, 1987a,b,c).

Among the products of the CWS research venture are thorough data on the diet composition and feeding rates of Common and Thick-billed Murre chicks. Birkhead and his colleagues found that Common Murre chicks subsisted mainly on capelin (*Mallotus villosus*), a high energy density, pelagic schooling fish. In contrast, they observed that Thick-billed Murres fed their young mostly daubed shanny (*Lumpenus maculatus*), solitary denizens of the benthos (Birkhead and Nettleship, 1987b).

During the hiatus in research between the end of Birkhead's and Nettleship's study in 1983 and the beginning of mine in 1996, whole movements in the symphony of the northwest Atlantic ecosystem were re-written. In response to a combination of oceanographic change and over-exploitation by humans, the abundances and distributions of many fish species changed (Mann and Drinkwater, 1994; Drinkwater, 1996). Included in the list of stocks affected by ecological changes in the 1990s was an important component of the Gannet Islands murres' chick diets: capelin.

Data from acoustic surveys conducted by the Canadian Department of Fisheries and Oceans (DFO) reveal a precipitous drop in the biomass of capelin in the waters near the Gannet Islands during the early 1990s (Miller and Lilly, 1991; Miller, 1993; Anderson, pers. comm) . Between 1981 and 1992, the DFO ran fall transects "listening" for capelin in North Atlantic Fisheries Organization (NAFO) fisheries management division 2J3K, which encompasses the nearshore waters from just north of Fogo Island, Newfoundland to Hamilton Inlet, Labrador (Figure 1.1). Despite wide between-year variation in estimates of capelin biomass in 2J3K, until 1989 the biomass near the Gannet Islands was uniformly high. As the overall biomass began to shrink in 1989, the distribution of capelin in 2J3K

shifted southward, such that the thinned-out ranks of fish virtually evacuated waters near the Gannet Islands and concentrated themselves south of the Strait of Belle Isle (Miller, 1993; John Anderson, pers. comm.) Cartwright fishers' observations corroborate DFO's capelin biomass estimates. Since the early 1990's, Cartwright residents report, capelin have spawned in smaller numbers and on fewer beaches than they had previously.

In the wake of these changes to the abundance and distribution of capelin in southern Labrador, I joined a small group of Memorial University and Atlantic Cooperative Wildlife Ecology Research Network (ACWERN) biologists re-establishing a research program on the Gannet Islands. We knew that the north west Atlantic's symphony would sound different than it had 15 years ago, but we were not sure how. I listened for the new harmonies related to murre chick diet by searching for answers to a suite of related questions. I wondered whether and to what extent the murres' chick diet had changed since the early 1980s. If their diets had indeed changed, I wondered whether this reflected changes in capelin abundance. I also wondered if potential diet changes would be concomitant with changes in other parameters, such as feeding rates, productivity, chick growth, adult mass and parental effort. Finally, I wanted to know if the ecologically similar Common and Thick-billed Murres partitioned or shared their chick-diet resources.

The question of how murres' behaviour or breeding parameters correspond to the abundance of their prey stems from a long tradition of people using seabirds as indicators of marine resources. Fishing people have customarily looked to birds for signs of the presence of target fish species. For example, gulls feeding at the sea surface signified the presence of mackerel shoals to Southern California fishermen, while gulls in the company of pelicans signified schools of anchovy (Soule, 1998). Scientists, too, are interested in how seabirds can be used to indicate the presence or absence of prey, as well as gauge their abundance and distribution. Many recent studies have correlated changes in seabird

behaviour and breeding success with oceanographic and marine ecological change. In the Barents Sea, Barrett and Krasnov (1996) showed that changes in the abundance of herring (*Clupea harengus*) were mirrored by changes in the breeding success of seabirds there. Uttley *et al.* (1989) showed how the reduction of sandlance (*Ammodytes sp.*) availability adversely effected the chick growth and breeding success of Common (*Sterna hirundo*) and Arctic Terns (*Sterna paradisaea*) on the Shetland Islands, UK. Also on the Shetland Islands, Monaghan *et al.*. (1996) demonstrated that between-year differences in Common Murre foraging behaviour and Black-legged Kittiwake (*Rissa tridactyla*) breeding success were dependent upon interannual variation in sandlance abundance in the vicinity of the colony. Similarly, the reproductive success of five seabird species breeding at the Farallon Islands, California was linked to the availability of rockfish (*Sebastes spp.*) (Ainley *et al.*, 1995).

Although these studies convincingly established correspondences between the behaviour and biology of seabirds and the abundance of their prey, one could argue that such correspondences offer little predictive value. That is, the birds' diet, productivity or chick growth can only crudely (on a nominal or ordinal, rather than an interval scale) forecast the distribution or biomass of marine prey (distinction in Cairns, 1987; Montevecchi, 1988; Montevecchi and Berruti, 1991). However, some studies have established more sophisticated and quantifiable linkages between seabirds and fish availability. For example, Montevecchi and Myers (1995; 1996) showed that the proportion of mackerel (*Scomber scombrus*) and short-finned squid (*Illex illecebrosus*) in the diet of Northern Gannets (*Sula bassana*) breeding in Newfoundland, Canada indicates the availability of these fish to Newfoundland fishers. Crawford and Dyer (1995) detected a close correlation between the biomass of spawning anchovies (*Engraulis capensis*) and the number of African Penguin (*Spheniscus demersus*) chicks fledged per nest at a South African colony. Moreover, they found that the proportion of South African sardine

(*Sardinops sagax*) in the chicks' diet could reliably predict deviations from the expected numbers of immature penguins recruited to the colony in the following year. Hatch and Sanger (1992) discovered that the distribution, growth rates and cohort strength of first-year walleye pollock (*Theragra chalcogramma*) in the Gulf of Alaska might be reliably indexed by the proportions and ages of pollock in the diets of Horned and Tufted Puffin (*Fratercula corniculata and F. cirrata*) chicks at a number of colonies along the Gulf's western edge. Furthermore, the number of Arctic Tern chicks banded each year at the Shetland Islands was significantly correlated with and could accurately predict the recruitment of 0-group sandlance to the Shetland population (Monaghan *et al.*, 1989).

The parameters measured by the above studies made good indicators because they satisfied (at least partially) the three criteria that Cairns (1992) identified as necessary for indexing fish stocks. For one, they responded directly to variation in stock size and this variation was not confounded by interacting variables. Second, they were sensitive to changes in stock size/distribution at all levels of stock size. Last, they yielded indices that were linearly correlated to stock size.

Ecological systems are not comprised of one-dimensional relationships, just as symphonies are not duets; the horn responds not only to the flute's part, but to those of the violin, clarinet, percussion etc. Likewise, seabird reproductive parameters potentially reflect not one, but myriad sources of variation - from environmental fluctuations to social phenomena to evolutionary constraints. For polyphagous seabirds, such as murres, researchers must not only tease out the parameter that best gauges fish abundance, they must also establish which fish stocks the parameter is sensitive to. As long-lived birds with delayed maturity, obligate one-egg clutches, generalist diets and discretionary time, murres could be expected to buffer the effects of changes in prey availability on productivity by changing chick diet composition and allocating more time to foraging (Cairns, 1987, 1992; Burger and Piatt, 1990). This suggestion has been supported by observations of Common

Murres in variable prey regimes by Burger and Piatt (1990), Monaghan *et al.* (1994, 1996) and Uttley *et. al.* (1996). These studies found that changes in the murres' activity budgets registered fluctuations in prey abundance, but the birds' productivity remained unchanged. However, no linear relationships between activity budgets and prey abundance were detected such that measurements of the former could be used to reliably predict levels of the latter.

In the next chapter, *Responses of Common and Thick-billed Murres' to changes in prey availability at the Gannet Islands,* I describe the effects of diminished capelin abundance on the murres' reproductive parameters. I examine whether and to what degree the murres' chick diet and feeding rates, productivity, chick growth and adult mass reflect the demonstrated decrease in capelin abundance near the islands, and I speculate as to how this decrease might account for the levels of parental effort I inferred from the amount of time pair members spent together at their site during chick feeding visits .

The second line of ecological harmonies into which I inquired was that which might emerge from the relationship between Common and Thick-billed Murre foraging behaviour. I investigated this because the diets and foraging behaviours of sympatric congeners can be influenced by each other, as well as by prey availability. This is because behaviour, morphology and physiology tend to forestall competition for resources. An indisputable scarcity of resources was one of the precepts from which Darwin (1859) argued for the Principle of Natural Selection. He wrote: "... there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life. It is the doctrine of Malthus applied with manifold force to the whole animal and vegetable kingdoms." Gause's (1934) law exemplifies twentieth century ecology's adherence to both Darwin's logic and the

Malthusian doctrine from which it stemmed. Also known as the competitive exclusion principle, Gause's law states that when they occur in sympatry, two ecologically similar species cannot exploit the same suite of resources.

Gause's law has been upheld by the results of numerous studies. For example, Lack (1947) documented that the bill sizes and foraging behaviours of syntopic species of Darwin's Finches diverged. MacArthur (1958) found that five species of warblers in the same coniferous tree partitioned their resources by foraging from different levels in the canopy and at different distances from the trunk. Similarly, Schoener (1968, 1970) described how different species of *Anolis* lizards while foraging perched on different portions of the limbs of the same tree. In another classic study, Cody (1968) demonstrated that habitat preferences and feeding behaviours differed among sympatric bird species on the grasslands of both North and South America. Seabirds, too, have been the subjects of resource partitioning research. Chinstrap, Gentoo and Adélie Penguins (*Pygoscelis antarctica*, *P. papua* and *P. adelie*) breeding on King George Island, Antarctica appeared to avoid high dietary overlap (Trivelpiece *et al.*, 1987). A study conducted by Barrett and Furness (1990) on alcids breeding in the Barents Sea revealed that sympatric murres, Razorbills and Atlantic Puffins distributed their capelin exploitation by taking fish at different depths and of different size classes. Cody (1973) purported to show that different auk species forage at different distances form their colonies.

Despite such definitive evidence for resource partitioning, in many cases diet segregation has proven illusory. Bédard (1976) disproved Cody's conclusion about resource partitioning between sympatric auks. Wilson (1995) conducted an experiment on Pygoscelids on the South Shetland Islands, similar to Trivelpiece *et al.*'s., but found more evidence for food resource overlap than for partitioning. Although Barrett and Furness demonstrated partitioning among murres, Razorbills and Puffins, Barrett et al. (1997) reported substantial dietary and dive-depth overlap between Common and Thick-billed

Murres. Wiens (1989) attributed food niche -overlap among seabirds to situations that violate Malthus' doctrine, ones in which prey are "seemingly superabundant."

Yet both superabundant and scarce prey could lead to increased diet overlap between sympatric predators (Pianka, 1981; Schoener, 1974). Although the overall availability of the murres' prey near the Gannet Islands remains unknown, the recent local decline in capelin abundance led me to ask: would Common and Thick-billed Murres' chick diets overlap more or less after the decline? In Chapter 3, *Food resource use by Common and Thick-billed Murres breeding at the Gannet Islands, Labrador*, I address this question by examining the possibility that Common and Thick-billed Murres might have exploited the same food resources. To do this, I present the extent of chick-rearing period overlap, chick-diet overlap, timing of feeding convergence, similarity of sizes and reproductive states of fish in chicks' diets, and maximum dive depth similarity between the two murre species.

The sources of variation - or harmonies- I describe in this thesis might be inextricable. That is, the murres' responses to changes in capelin abundance and their putative responses to each others' food resource use are probably interdependent. I address this in the concluding chapter, in which I test the strength of the links between resource availability, resource use and competition both in general and between Common and Thick-billed Murres breeding at the Gannet Islands.

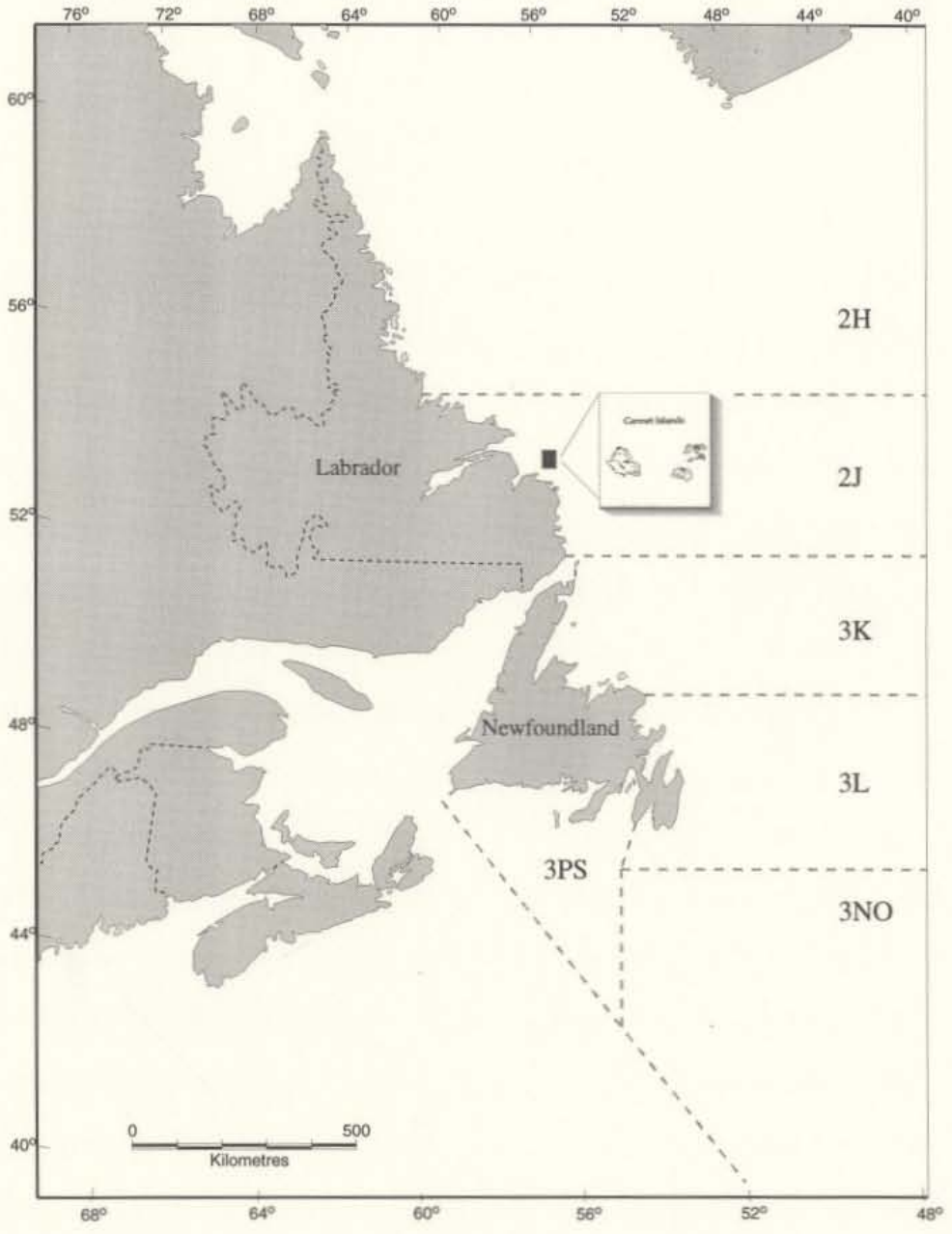

Figure 1.1: Map of Atlantic Canada showing location of Gannet Islands and North Atlantic Fisheries Organization (NAFO) fisheries management divisions 2H, 2J, 3K, 3L, 3NO and 3PS

CHAPTER 2

RESPONSES OF COMMON AND THICK-BILLED MURRES TO CHANGES IN PREY AVAILABILITY AT THE GANNET ISLANDS

2.1 ABSTRACT

I measured Common and Thick-billed Murre chick diets, feeding rates, breeding success, chick growth, adult masses and pair members' time spent together at site (TAS) after a decline in the abundance of capelin along the coast of southern and central Labrador. With the exception of TAS, I compared these results with those collected by other researchers at the same site in 1981-83, before the capelin decline. After the decline, murres fed their chicks up to 75 per cent less capelin and up to 65 per cent more daubed shannies than they had fifteen years previously. Feeding rates of both species varied by up to 250 per cent among the five years, but this variation was not concomitant with changes in the proportion of capelin in the chicks' diets. The murres' dietary shift did not seem to affect their colony attendance adversely; counts of both murres on some plots increased, while on others they did not differ significantly. Neither murre species had lower breeding success after capelin became scarce. Chicks of both species grew well following the decline in capelin availability. Masses of adult murres were not significantly different after capelin became scarce than they were before. No time-at-site data were taken before the decline in capelin abundance, but after the decline off- duty Common and Thick-billed Murres both spent a mean of ten minutes at their sites per feeding visit. This amount of time was lower than that recorded for Common Murres elsewhere, suggesting that murres' foraging effort at the Gannet Islands was high and buffered the effects of prey availability on other parameters measured.

2.2 INTRODUCTION

Changes in prey availability can profoundly affect reproductive parameters of breeding animals. Breeding seabirds have been shown to respond to variation in availability of their marine prey with changes in chick diet composition (e.g., Northern Gannets *Sula bassana*, Montevecchi and Myers, 1995 ; Cape Gannets *Morus capensis* (Crawford and Dyer, 1995, Little Penguins *Eudyptula minor*, Cullen *et al.* 1992, Hobday, 1992), feeding rates (Common Murres, Uttley *et al.*, 1994) clutch size (Black-legged Kittiwakes *Rissa tridactyla*), productivity (e.g., Brown Pelicans *Pelicanus occidentalis*, Anderson and Gress, 1984; African Penguins *Spheniscus demersus* and Cape Gannets, Crawford and Dyer, 1995; Black-legged Kittiwakes, Monaghan *et al.* 1996, Atlantic Puffins *Fratercula arctica*, Barrett, 1996, Little Penguins, Cullen *et al.*, 1992; Hobday, 1992) colony attendance (e.g., Common and Thick-billed Murres, Vader *et al.* 1990, Cape Cormorants *Phalacrocorax capensis* and Swift Terns *Sterna bergii*, Crawford and Dyer, 1995) time-activity budgets (e.g., Common Murres, Burger and Piatt, 1990, Cairns 1992, Monaghan *et al.*, 1992, 1994, Black-legged Kittiwakes, Monaghan *et al.*, 1992, 1994a; shags *Phalacrocorax aristotelis*, Monaghan, *et al.*,1992, 1996), chick growth (e.g., Atlantic Puffins, Barrett 1994; Little Penguins, Cullen et al, 1992) adult mass (e.g., Black-legged Kittiwakes, Monaghan *et al.*, 1996) and survival (e.g., Common and Thick-billed Murres, Vader et al, 1990).

Alcids are long-lived birds with delayed maturity, and thus can afford to adjust their reproductive effort as environmental conditions change (Lack, 1968). As pursuit diving alcids with obligate one-egg clutches, murres could be expected to adjust foraging effort and chick diet composition before limiting their clutch size or affecting chick's

growth. In fact, in the wake of less than catastrophic changes in prey availability, this has been evinced (Burger and Piatt, 1990; Monaghan *et al.*, 1994, 1996; Uttley *et al.*, 1996).

Multi-year studies of seabird reproductive performance and prey abundance are necessary to test hypotheses about the birds' responses to changes in prey availability. This type of integrated research was possible at the Gannet Islands, Labrador, where during the early 1980s, T.R. Birkhead and D.N. Nettleship systematically gathered data on Common and Thick-billed Murre chick diet composition, feeding rates and productivity. They also collected information pertaining to chick growth, colony attendance and adult mass. In the eighties, capelin had predominated Common Murre chick diet and had been important to Thick-billed Murre chick diets (Birkhead and Nettleship, 1987c). After the conclusion of their research 1983 and before the inception of this study in 1996, capelin virtually evacuated southern and central Labrador waters and ceased spawning on beaches near the Gannet Islands (Miller, 1993; J. Anderson, pers. comm.; Cartwright residents, pers. comm.).

With this study, I sought to determine directly the extent to which Common and Thick-billed Murre chick diet composition, feeding rates and productivity reflected changes in capelin availability at the Gannet Islands. I also attempted to asses indirectly the effects of such changes on colony attendance, chick growth and parental time budgets. Since Common Murre chicks had previously depended more heavily on capelin than Thick-billeds had I hypothesized that Common Murre parameters would exhibit more sensitivity to changes in the fish's abundance.

2.3 METHODS

2.3.1 Study site

I conducted this research on GC4, one of seven small islands comprising the Gannet Islands Ecological Reserve. Located approximately 60 km west of the highly productive Hamilton Bank, the Gannet Islands (53° 57' N 56° 31' W) host Labrador's most diverse seabird colony. About 47,000 and >6,000 pairs each of Common and Thick-billed Murres spend their breeding seasons at the Gannet Islands (Lock *et al* . 1994). In addition, the islands are home to about 39,000 pairs of Atlantic Puffins *Fratercula arctica*, 6,400 pairs of Razorbills *Alca torda*, 110 pairs of Black Guillemots *Cepphus grylle* (Lock *et al*, 1994) and smaller populations of Common Eiders *Somateria mollissima*, Northern Fulmars *Fulmaris glacialis*, Black-legged Kittiwakes, Great Black-back Gulls *Larus marinus* and Herring Gulls *Larus argentatus*. An unknown number of Leach's Storm Petrels *Oceanodroma leucorrhoa* breed at the Gannet Islands, as well.

Co-occurance of high numbers of both murre species is relatively rare at colonies in the North Atlantic. Generally, the congeneric murres are geographically segregated during their breeding season; Common Murres tend to reside at lower latitudes than Thick-billeds do. However, the murres' ranges overlap at the Gannet Islands, rendering this site an ideal place to compare these closely related species.

In 1996 and 1997, I repeated and expanded the previous researchers' protocol (Birkhead and Nettleship, 1987a,b,c,) for studying murre chick diet, feeding rates, breeding success, chick mass, adult mass and colony attendance. In addition, I measured the amount of time both members of a pair spent together at their site per feeding visit during the chick rearing period.

2.3.2 Breeding success

I monitored murres' productivity to compare their reproductive performance both between species as well as within species and between years. Sites for productivity monitoring were chosen because they were located in the same part of the colony as Birkhead's and Nettleship's plots Common Murre A and Thick-billed Murre A (Birkhead and Nettleship, 1987a,b), and because they could be observed without noticeably disturbing birds. I monitored 180 Common Murre sites for productivity in 1996 and 140 sites in 1997. These sites occupied about $15m^2$ of a boulder-strewn rock platform approximately 5m above sea level and 30m from the sea. Using 7x binoculars and a 20x spotting scope, I watched the birds from a blind perched approximately 15 meters above the plot. The murres appeared to be unaware of and undisturbed by observers entering, sitting in or leaving the blind.

Mark Hipfner monitored 150 Thick-billed Murre pairs in both 1996 and 1997. These birds held sites on cliff ledges and steep rocky slopes above and to the south of the Common Murre plot. The occupied portions of the cliffs and slopes stood about 25 m above sea level. Using a 20x spotting scope, he watched Thick-billed Murres from a blind approximately 15-30 m across a gulch from their sites. Like the Common Murres, the Thick-billed Murres did not respond to observers entering, sitting in or leaving the blind.

We mapped these study plots and numbered the nest sites on them. Every day during the breeding season, we checked each site on the plots and recorded whether there was an egg, a chick or nothing present. Thus for most sites I could determine the chicks' hatching and fledging dates to within 24-hours and reliably establish the percentage of eggs that hatched and percentage of chicks that fledged. To determine hatching success, I calculated the percentage of eggs laid that hatched. Likewise, fledging success was the

percentage of chicks that fledged from hatched eggs. Breeding success was the product of hatching and fledging success.

To make inter-year and interspecies comparisons of Common and Thick-billed Murre productivity, I used Chi-Square tests.

2.3.3 Colony attendance

Mark Hipfner and I counted adult murres present on five count plots at 16 h every two to three days during the breeding season in 1996 and 1997. Three of the plots we counted were identical to those counted by Birkhead and Nettleship in 1981 (Birkhead and Nettleship, 1982). These were Thick-billed A and C and Common C. On each plot, we tallied the number of murres twice. If the two counts were within five per cent of each other, we averaged them. If not, we made a third or fourth count then averaged the two most similar counts.

2.3.4 Diet composition and feeding rates

Totals of 10-60 (depending on how many chicks had hatched or fledged) of the Common Murre sites and 15-30 of the Thick-billed Murre sites monitored for productivity were also monitored for chick diet composition and feeding rates. At regular intervals throughout the chick-rearing period, I conducted four-hour feeding watches with the help of other field researchers. Two people conducted each watch; one would record Common Murre food deliveries between 1400h and 1800 h, while the other would record Thick-billed Murre food deliveries. For each food delivery, we recorded the time, the site number and the species of fish delivered. Murre chicks' meals invariably consisted of a single undigested fish. Holding these fish lengthwise in their bills (such that the fish dangle out of the birds' bills), parents walked or flew from the sea to their site. In most cases we

were able to identify fish during this traveling period. In some cases, we identified fish as chicks paused before ingesting them. We used 20x spotting scopes to identify Thick-billed Murre chicks' fish and 7x binoculars or our naked eyes to identify Common Murre chicks' fish. our identifications were corroborated by diet samples collected directly from birds and from prey dropped on breeding ledges at other parts of the colony (see Methods , Chapter 3).

In 1996 eight Common and eight Thick-billed Murre four-hour feeding watches were conducted. In 1997 11 Common and nine Thick-billed Murre four hour feeding watches were conducted.

To account for differences in mass among prey items, I converted the percentages-by-number of chick diet items to percentages by mass. I used the mean masses of capelin, daubed shannies (*Lumpenus maculatus*), sandlance (*Ammodytes hexapterus*), sculpin (*Myxocephalus sp.*) and fish doctors (*Gymnelis viridis*) collected from Common Murre parents in 1996 to make the conversions for 1996, and the mean masses of capelin and daubed shannies collected in 1997 to make the conversions for that year. Some of the prey species relegated to the "other" category (such as squid (*Illex sp.*) and Atlantic cod (*Gadus morhua*)) recorded during feeding watches were never collected from adults; these were not used to calculate mean percentages by mass.

Daubed shannies in 1997 were the only intact fish collected from Thick-billed Murres. I assumed that the masses of these fish were the same in 1996 as in 1997 (this assumption held true for Common Murres' shannies, $t = 1.4$, $df = 176$, $p = 0.16$) and that the masses of the capelin delivered to Thick-billed Murre chicks were the same as those delivered to Common Murres.

I used logit loglinear analyses to compare between years the predominance of the most important items in the diets of chicks. Using this method, I determined whether the

odds of a parent of one murre species delivering a given type of fish were significantly different in one year than in another, and whether the odds of delivering a given type of fish varied between murre species.

2.3.5 Chick growth

In 1996 I took a single mass and wing measurement from 36 Common Murre chicks of unknown age. Chicks were chosen for measurement because they occupied sheltered sites, such that they could be handled without causing nearby chicks to fledge prematurely. Five of the chicks I measured in 1996 had wing lengths of 60 mm or greater. Following Birkhead and Nettleship (1984), I assumed these chicks to be at least 20 days old and considered their masses to be fledging masses, which I used as an index of chick growth. In 1997, Mark Hipfner weighed and measured 9 Common and 8 Thick-billed Murre chicks of known age every three days from hatching until fledging. From these measurements, I calculated the chicks' maximum growth rates (g/day) and mid-point weights (median of hatch and fledge weights). In both years, mass measurements were taken to the nearest gram using a 300g spring scale. Wing measurements were made to the nearest millimeter from the birds' carpal joint to the tip of their longest primaries.

2.3.6 Adult mass

Within-season changes in adult murres' mass might result from adaptive weight loss, an increase in exercise, or a combination of both (Croll *et al.* 1991). If murres' mass varies with the amount of energy they expend, then mass differences within a single population but between years could indicate inter-year differences in prey availability (Monaghan, 1996). In order to compare the masses of murres during incubation with those during chick rearing, and to compare between years the masses of chick-rearing murres, I

weighed both Common and Thick-billed adults throughout their breeding seasons in 1996 and 1997. Other researchers and I used noose poles to capture Thick-billed Murres and both noose poles and fleyg nets to capture Common Murres. In 1996, 71 incubating and 46 brooding Thick-billed Murres were weighed. In 1997, 23 incubating and 11 brooding Thick-billeds were weighed. Only the masses of the Thick-billed Murres of whose breeding stage (incubating or brooding) I was certain were included in my analyses. In 1996 incubating Common Murres were not weighed, but 106 brooding Common Murres were weighed. In 1997, 13 brooding and 64 incubating Common Murres were weighed. I assumed that the Common Murres caught in the fleyg net were brooding chicks because they all were carrying fish to the colony and I rarely saw non-brooding Common Murres bring fish to the observation plots during the chick-rearing period. Murres were not caught on or in the vicinity of the feeding watch/productivity plots.

To compare murres' incubation and brooding masses, I used unpaired, two-tailed t-tests. To compare brooding masses for each murre species between years, I used one-way ANOVAs.

2.3.7 Time at site

As a proxy for measuring the amount of time murres allocated to foraging, I measured the time both members of a pair remained together at their site after the parent on foraging duty arrived with a chick meal. Time-at-site (TAS) has been shown to indicate both foraging trip length and foraging effort (Monaghan *et al.*, 1994). To establish Thick-billed and Common Murres' mean TAS, Aléjandra Nuñez de la Mora and I conducted focal pair (FP) watches. FP watches were conducted opportunistically, during all daylight hours. We began a FP watch when a bird arrived at its site with a fish, thus ensuring that the birds we were watching were truly a pair. FP watches ended when one of the pair members left

the site. By subtracting parents' arrival times from departure times, I determined to the nearest minute the amount of time off duty birds spent at their site per visit. I never saw a Common or Thick-billed Murre spend time at the colony away from the vicinity of its site, except for the short time Common Murres sometimes spent walking directly from their site to the water or vice versa. However, if the murres frequented parts of the colony away from their sites without first spending time at their sites, we would not have detected it.

To determine whether off-duty Common or Thick-Billed Murres varied the amount of time they spent at their sites with respect to time of day or part of chick rearing period (early, middle, late) I used ANOVAs. I used two-tailed unpaired t-tests to compare the amounts of time Common and Thick-billed Murres spent at their sites.

2.4 RESULTS

2.4.1 Breeding success

Thick-billed Murres consistently experienced lower breeding success than Common Murres. In 1996, this difference was not significant (X^2 = 1.16, df= 2, p= 0.56), but in 1997 it was (X^2= 8.86, df= 2, p= 0.01; Tables 2.1 and 2.2, Figure 2.1). In 1996 and 1997 Common Murre breeding success was between 83 (n=139) and 85 (n=109) per cent, while Thick-billed Murre breeding success was between 51 (n=144) and 71 (n=143) per cent. The difference between Common and Thick-billed Murre hatching success was significant in 1997 (X^2= 14.13, df=1 , p< 0.001) but not in 1996 (X^2=0.81, df= 1 p= 0.39). In both years, between-species differences in fledging success were not significant (1996 X^2= 0.04, df=1, p =0.85; 1997 X^2= 0.83, df=1, p= 0.38).

Neither Common Murres' nor Thick-Billed Murres' breeding success varied among the years 1981, 1982, 1983, 1996 and 1997 (fig.3 and 4, Table 3 and 4; Common hatching

success X^2= 1.09, df= 6, p= 0.99 fledging success X^2=0.16, df=6, p=0.99; Thick-billed hatching success X^2 = 1.86, df= 6, p=0.99 fledging success X^2=0.63, df= 6, p=0.99).

2.4.2 Colony attendance

The mean numbers of Thick-billed Murres counted in 1996 were twice as high on one plot and did not different significantly on another with respect to counts made in 1981 (Table 2.3). The mean number of birds present on plot Thick-billed-A increased significantly from 93 in 1981 to 196 in 1996 (t= 16.74, df= 69, p<0.0001). On plot Thick-billed-C, the mean number of birds did not vary between years (t= 0.10, df= 67 p=0.9).

The mean number of Common Murres present on count plot Common-C increased significantly from 101 in 1981 to 121 in 1996 (t= 16.38, df=66,p<0.001) (Table 2.3).

2.4.3 Diet composition

In both 1996 and 1997, shannies accounted for the bulk of Common and Thick-billed Murre chick diets (Figure 2.2, Tables 2.4 and 2.5). Shannies comprised 84 (n=397) and 53 (n=404) per cent by number of Common Murre chick diets in 1996 and 1997 respectively. With respect to mass, shannies' contribution was slightly lower; in 1996 the fish made up 79 per cent and in 1997, 48 per cent of the masses of Common Murre chick diets. Capelin was the second most common item in the chicks' diet. In 1996 capelin made up 12 per cent by number and an estimated 13 per cent by mass of Common Murre chick diet. In 1997 capelin accounted for 45 per cent by number and 50 per cent by mass of the chicks' meals. The results from loglinear analyses showed that the chances of a Common Murre feeding a capelin to its chick in 1996 were smaller than they were in 1997; the log of the odds of a capelin delivery were significantly higher in 1997 than in 1996 (Table 2.6, 2.7). Conversely, the chances of a shanny feed were greater in 1996 than they were in

1997, as the log of the odds of a shanny delivery was higher in the first year. In both years, fish other than capelin and shannies accounted for small proportions of Common Murre chicks' diets. Other fish in the Common Murre chicks' 1996 and 1997 diets included sandlance, *Ammodytes hexapterus* , fish doctor, *Gymnelis viridis*, Atlantic cod *Gadus morhua*, Arctic Cod (*Boreogadus saida*) sculpin (*Myxocephalus sp.*), and squid (*Illex sp.*).

The Thick-billed Murre chicks' diets were composed of more shannies and fewer capelin than the Common Murres' (Figure 2.3, Tables 2.8 and 2.9). In 1996 and 1997, shannies comprised 97 (n=234) and 94 (n=244) percent by number, and 96 and 93 per cent by mass of their diets. Capelin accounted for the remaining 2 to 6 per cent by number and 3 to 8 per cent by mass. The logs of the odds of both capelin and shanny deliveries to Thick-billed murre chicks were similar in both years (Tables 2.10, 2.11). Thus, the chances of a delivery of each type of fish were the same in 1996 as they were in 1997.

In 1982 and 1983 Thick billed Murre chicks were sometimes fed Arctic cod, fish doctor and sandlance (Birkhead and Nettleship, 1987c), but during feeding watches in 1996 and 1997, observers recorded no fish other than capelin and shannies being delivered to Thick-billed chicks. In both years, however, we made rare incidental observations of Thick-billed Murres feeding Arctic cod to their chicks.

The results of logit loglinear analyses show that in 1996 and 1997, as in the eighties, the chances of a Common Murre feeding a capelin to its chick were greater than the chances of Thick-billed capelin feed. The opposite held true for shanny feeds. In each year, the log of the odds of a Thick-billed Murre delivering a shanny to its chick were higher than those of a Common Murre delivering one.

Despite these consistent interspecies differences in the ratios of chick diet items, changes in the chick diets of both murres exhibited similar patterns. Parents of both species fed their chicks substantially more shannies and fewer capelin and Arctic cod in 1996 and

1997 than they did in 1982 and 1983 (Tables 2.12, 2.13, 2.14, 2.15). The results of logit loglinear analyses reflected the murre chicks' dietary shift. The log of the odds of a member of either murre species delivering a capelin to its chick were significantly higher in 1982 and 1983 than they were in 1996 and 1997 (Tables 2.7 and 2.11). Conversely, for both species, the log of the odds of a parent delivering a shanny were higher in the nineties than they were in the eighties.

2.4.4 Feeding rates

In 1996, Thick-billed Murres fed their chicks more frequently than in 1997 ($t=5.49$, $df=16$, $p<0.00001$). Common Murres exhibited a similar between-year difference in feeding rates, but the difference was not significant ($t=1.97$ $df=18$, $p=.06$). Thick-billed Murres fed their chicks at a significantly higher rate than Common Murres in 1996 ($t=6.58$, $df=14$, $p<0.00001$). However, in 1997, the murres' feeding rates did not differ significantly ($t=1.50$, $df=20$, $p=0.15$).

Common and Thick-billed Murres' feeding rates varied significantly among the years 1981, 1982, 1983, 1996 and 1997 (Figures 2.4 and 2.5; Common Murre $F_{(4,48)} = 58$, $p<0.0001$; Thick-billed Murre $F_{(4,47)}= 69.2$ $p<0.0001$). The results of post-hoc t-tests comparing feeding rates between each possible pair of years revealed that some between-year differences in feeding rates corresponded loosely with the amount of capelin in the birds' diets, although such correspondence is inconsistent. Feeding rates for both species peaked in 1996, when the proportion of capelin in their diets reached its nadir. The murres' feeding rates were lowest in 1981, but little chick diet information was available for that year. Differences in both murres' feeding rates between 1982 and 1983 corresponded with differences in the percentage by mass of capelin in their respective diets (Birkhead and Nettleship, 1987c).

When comparing 1997 feeding rates to those from 1982 or 1983, I found no relationship between the proportion of capelin in the chicks' diets and feeding rates. Feeding rates in 1997 were as low as or lower than those reported by Birkhead and Nettleship (1987c) for the early eighties, although the percentage of capelin in the chicks' diets was also lower.

2.4.5 Chick growth

In 1996, the mean mass of previously undisturbed Common Murre chicks with wing lengths of greater than or equal to 60 mm was 233 +/- 21g (n=5), or 24 per cent of adult mass. The mean fledging mass of regularly handled Common Murre chicks in 1997 was 223 +/- 21g (n=8), which was 23 per cent of mean adult mass in that year. The mean fledging mass of regularly handled Thick-billed Murre chicks in 1997 was 224 +/- 25g (n=8), or 24 per cent of the mean adult mass in that year.

The maximum growth weights, mid -point weights (median of hatching weight and peak weight) and fledge weights of Common and Thick-billed Murre chicks at the Gannet Islands in 1997 were high compared with those from other colonies (other colonies' data compiled by A. Gaston, 1985a; Tables 2.16 and 2.17). When expressed as percentages of adult mass, the fledge weights of Thick-billed Murres at the Gannet Islands were as high as or higher than those at other colonies, and those of Common Murres were average.

Because of differences in methodology, I can only make a direct comparison of Common Murre chick fledging masses at the Gannet Islands for one pair of years: 1981 and 1996. No significant difference existed between the murres' mean fledging masses in these years ($t = 0.79$, $p < 0.05$). However, the 1996 sample size was small (n=5). The measurements taken on both murre species in the 1980s were made only on peak fledging nights on chicks that were undisturbed until they fledged, and those taken in 1997 were

made throughout the fledging period on chicks that were handled regularly. In 1982 and 1983 the mean fledging masses of previously undisturbed Common Murre chicks were 232+/- 21 g (n= 52) and 246+/-31 g (n=94), respectively (Birkhead and Nettleship, 1985), up to 15 g (or 7 per cent) higher than that of regularly handled chicks in 1996 and 1997. In 1983, the mean mass of fledging Thick-billed Murres was 228+/- 30 g (n=10), only 0.2 per cent higher than that of regularly handled Thick-billed Murre chicks in 1997.

2.4.6 Adult mass

For both Common and Thick-billed Murre adults, masses during chick rearing tended to be lower than incubation masses (Tables 2.18 and 2.19). In 1996, the mean mass of adult Thick-billed Murres during incubation was 5 per cent lower than it was during chick-rearing. This difference was significant (t=3.64, df=115, p=0.004). In 1997, the mean mass of incubating Thick-billed Murres was 2.6 higher than that of chick-rearers. This difference was not significant (t= 1.03, df=32, p = 0.31). The mean mass of chick-rearing Common Murres in 1997 was 5% higher than the mean mass during incubation. This difference was significant (t=2.30; df=75, p= 0.02).

The mean mass of chick -rearing Thick-billed Murres varied significantly among the years 1981, 1982, 1996 and 1997 ($F_{(3,103)}$ = 2.9 p= 0.04). This variation can be attributed to an exceptionally high mean mass during the chick-rearing period in 1997. There was no interyear variation in the masses of chick-rearing Common Murres ($F_{(4,249)}$ = 1.54 , p=0.2).

2.4.7 Time-at-site

In 1997, Common Murre pair members spent a mean of 10.5 +/- 7.5 minutes (n=41) together at their sites during single feeding visits at their site. The median time they

spent together was 9 minutes, with an interquartile range spanning from 6 to 12 minutes. Thick-billed Murres spent similar, but more variable amounts of time together, staying with their mates for a mean of 11.3 +/-11.0 minutes per feeding visit. The median time Thick-billed Murres spent together was 7 minutes, with an interquartile range from 3 to 17 minutes (Table 2.20). Neither Common nor Thick-billed Murres on foraging duty varied the amount of time spent at their site with respect to time of day or time of season. (Thick-billed TAS with respect to season $F_{(2,26)}$=0.86, p=0.73; Thick-billed TAS with respect to time of day $F_{(2,\ 26)}$=1.1, p=0.49; Common TAS w/rep. to season $F_{(4,40)}$ =1.1, p=0.27; Common TAS w/ rep. to time of day $F_{(2,40)}$ =1.1, p=0.88). Thus, I was able to pool the data for each species and make an interspecies comparison of TAS.

I found no significant difference between the mean amount of time off-duty Common and Thick-billed Murres spent at their sites (t=0.361, df=66 p=0.72). (Figure 2.6) .

2.5 DISCUSSION

2.5.1 Breeding success

Despite inter-year variability in prey availability and chick diet composition, neither Common nor Thick-billed Murres' breeding success changed significantly between years. Monaghan *et al.* (1994) also found murre breeding success to be relatively insensitive to changes in prey availability.

During this study, Common Murres consistently experienced higher breeding success than Thick-billed Murres. This is a function of their differentially high hatching success, as both murre species had similar fledging success in both years. In 1981, 1982 and 1983 Thick-billeds at the Gannet Islands experienced both lower hatching and lower fledging success than Common Murres did (Birkhead and Nettleship, 1987b.) Birkhead

and Nettleship (1987b) attributed the murres' unequal hatching successes to differences in habitat. Although I observed very few egg loss events, I believe that habitat differences explain the interspecies difference in breeding success recorded in this study, as well. The Common Murres monitored in this study occupied flat or gently sloping rock platforms. If an egg were to roll from one of these sites, it would not go far and probably would not risk a fall. Eggs rolling from the narrow cliff ledges on which Thick-billeds laid, however, would more likely fall and break. Because chicks are more site-fast than eggs, this difference in habitat type would not effect chick mortality. Common and Thick-billed Murres breeding on Bear Island in the Barents Sea are segregated by habitat like Gannet Islands murres are, and displayed similar differences in hatching success (Williams, 1974). These cross-colony and cross-year differences in Common and Thick-billed habitat type and breeding success should not be reduced to interspecific variation, because similar disparities have been demonstrated within murre species but between habitat types. For instance, on Bylot and Coburg Islands in the eastern Canadian Arctic, Thick-billed Murres breeding on wide ledges bred more successfully than those occupying narrow ones (Birkhead *et al.*, 1985). Common Murres breeding on Tatoosh Island, Washington were less successful in some habitats than in others, but this was largely a function of predation, not egg -rolling (J.K. Parrish, 1995). Successful predation attempts on eggs or chicks of either murre species were observed extremely rarely at the Gannet Islands during this study.

2.5.2 Colony attendance

Colony attendance of Gannet Islands Murres did not fall in response to decreased abundance of capelin. In fact, the numbers of both species attending the colony probably increased between 1983 and 1996.

Unlike colony attendance of Gannet Islands murres, that of murres breeding in the Barents Sea varied in response to capelin abundance (Vader *et al.*, 1990). Concurrent with a collapse of the Barents Sea capelin stock, numbers of Common Murres breeding at three colonies in Northern Norway plummeted by about 80 percent. Thick-billed Murres at the same colonies fared better, although their numbers also fell substantially, by 33 to 63 per cent (Vader *et al.*, 1990). The difference in magnitude of murres' responses was attributed to differences in the feeding habits of adults, and to chick diet composition. Relying less heavily than Common Murres on capelin, adult Thick-billed Murres suffered lower mortality during winter. This differential mortality was reflected in different magnitudes of breeding colony attendance decline (Vader *et al.*, 1990).

Because murres are long-lived and can "choose" to forgo a breeding season at little cost to their lifetime fitness, their adult survival will only be affected by extreme prey shortages (Monaghan, 1996). The Gannet Islands Murres did not exhibit declines in colony attendance similar to their conspecifics in the Barents Sea probably because their food resource base changed less adversely and/or because both Common and Thick-billed Murres from the Gannet Islands were able to sufficiently supplement their winter diets with fish other than capelin.

Information on the wintering grounds, and winter feeding ecology of murres would be necessary to support or reject the latter possibility. The location of the wintering grounds of Gannet Islands Murres are unconfirmed. Nonetheless, it is reasonable to assume that in large part, the birds winter on the Grand Banks off Newfoundland. Birds from unspecified colonies in Labrador, as well as those breeding in both northerly and more southerly locales, spend at least part of the winter in this highly productive region (Tuck, 1960). In contrast to murres in the Barents Sea, Common and Thick-billed Murres wintering off the coast of Newfoundland exploit similar suites of prey items; historically, both subsisted

primarily on Arctic cod and capelin. Thick-billed Murres also ingested a substantial amount of crustaceans in the winter (Elliot *et al.*, 1987).

Although I am uncertain of the availability of prey to Gannet Islands Common and Thick-billed Murres in winter, it seems likely that even in the absence of pelagic fish, murres from the Gannet Islands wintering near the Grand Banks, or elsewhere, could survive on benthic creatures. This is because during the summer, Thick-billed Murres regularly fished for shannies and Common Murres were capable of switching from fishing for capelin to fishing for shannies for their chicks.

2.5.3 Diet composition

Common Murre chick diets predominated by benthic fish are anomalous and rarely documented. Their chicks' diets often include some demersal fauna, yet Common Murres tend to prey less upon benthic animals than on pelagic schoolers. For instance, the most prevalent items in Common Murre chick diet in the northwest Atlantic historically have been capelin (Burger and Piatt, 1990; Birkhead and Nettleship, 1987c; Bradstreet and Brown, 1985) and, less recently, sandlance (Tuck, 1960). The principal items in their diets in the Barents Sea were capelin, herring and sandlance (Furness and Barrett, 1985; Barrett and Furness, 1990; Barrett *et al.*, 1997). In the North Sea, Common Murre chick diet consisted mainly of sandlance (Harris and Wanless, 1995) and in the Irish Sea, it consisted mainly of sprat (*Sprattus sprattus*) (Hatchwell, 1991). Although Common Murre chick diets very rarely deviate from this trend, a benthic fish prevailed in the chick diet at the Farallon Islands (Ainley *et al.*, 1996). Common Murres at this colony fed their chicks juvenile redfish, which usually become demersal by the time they are large enough to appear in chick diets (Moser and Boehlert, 1991).

The change in Common Murre chick diet between 1982-3 and 1996-7 is striking not only for its magnitude, but for the behavioural flexibility it must have required. Because daubed shannies live solitarily in the benthos, murres must employ a different strategy to catch them then they do to catch the pelagic, schooling capelin. Foraging murres can set a course toward a school of fish by tracking conspecifics returning to the colony (Sergeant, 1951; Gaston and Nettleship, 1981) and then making repeat trips to the same school. In contrast, when preying on non schooling fish, birds must find their quarry individually and make a new search upon each foraging attempt. Benthic fish typically respond to predators by hiding in the substrate, whereas pelagic fish respond to predators by schooling tightly. Hence, a birds' tactics for catching benthic fish must differ markedly from its tactics for hunting pelagic fish.

Although the Thick-billed Murre chicks' dietary shift was similar to the Common Murres', a predominately benthic diet is less unusual for Thick-billed than for Common Murre chicks. The diets of Thick-billed Murre chicks often include sizable proportions of benthic fish as well as pelagic fish (Tuck, 1960; Bradstreet and Brown, 1985; Gaston, 1985b). Demersal fish are especially common in chick diets at colonies in the more southerly reaches of their Atlantic range, including the Gannet Islands in the 1980's (Bradstreet and Brown, 1985; Birkhead and Nettleship, 1987c). But a schooling fish, the Arctic cod, is the most prevalent item in their diets at both low and high arctic colonies in Eastern Canada (Gaston and Nettleship, 1981; Gaston, 1985b).

This change in Common Murre chicks' diet composition was not necessarily accompanied by a change in diet quality. Some data suggest that at the Gannet Islands, the energy density and fat content of daubed shannies are equally as high those of capelin. Proximate analyses were conducted on 12 daubed shannies and 2 capelin that I collected from chick-rearing Common Murres on the Gannet Islands in 1996 (please see chapter three for diet sample collection methodology). The analyses revealed that the lipid and

protein content, as well as the energy density of daubed shannies were as high as those of capelin (Alexandra Magalhaes, 1998). These parameters vary widely with fish sex and reproductive state, (Montevecchi and Piatt, 1984) and the Gannet Islands sample size was small. Yet the energy densities of the Gannet Islands murres' capelin were much higher than those derived from larger data sets (Montevecchi and Piatt, 1984). Taken together, the results from proximate composition studies suggest that daubed shannies might be equally nutritious as capelin for murre chicks. This contradicts the findings of Birkhead and Nettleship (1987), who reported that Gannet Islands murres' capelin had higher energy densities than daubed shannies. Their conclusion was based on the results of bomb-calorimetric analyses, which are less precise and more prone to error than proximate analyses.

Not only are there very few data on the daubed shanny's nutritional value, little research has been conducted on the fish's abundance, distribution, behaviour or ecology. An inkling of the daubed shanny's distribution can be gleaned from museum collections. The Smithsonian Institution, the Scripps Institute of Oceanography and the University of Washington hold samples of daubed shannies collected in waters from Alaska to Lake Melville, Labrador. For those samples for which there is information on the bottom depth at site of capture, all daubed shannies were collected from the benthos. The depths at which the fish were caught (0-120 m) fell within the range of depths to which I found chick-rearing murres at the Gannet Islands to dive (Scripps Institute of Oceanography Oceanographic Collections 1997; NMNH Fish Collection, 1998; UWFC Search Interface, 1998 and see Chapter 3).

These scant data only begin to suggest the daubed shanny's geographic range. Another study, the North Atlantic Strategic Assessment Project (SAP), conducted jointly by the National Oceanographic and Atmospheric Administration, U.S.A. (NOAA) and DFO, offers a preliminary and somewhat inchoate description of the relative abundances of

daubed shannies along the north eastern coast of North America. The results of SAP trawls indicated that daubed shannies are equally abundant along most of the coast, from northern Labrador to the southern Gulf of Maine, but are more abundant in the southwestern Gulf (East Coast of North America Strategic Assessment Project, 1998). Nonetheless, too few of SAP's trawls contained daubed shannies, and the mean number of daubed shannnies caught per tow was too low to afford reasonable estimates of the fish's real abundance.

2.5.4 Feeding rates

The rates at which both Common and Thick-billed Murres provisioned their chicks varied between years, but not in accordance with changes in the proportion of capelin in the chicks' diets. Similarly, Burger and Piatt (1990) found that in spite of within and among season fluctuations in capelin availability in and near Witless Bay, Newfoundland, Common Murres did not adjust the rates at which they fed their chicks. In contrast, at the Shetland Islands, Common Murre chicks' feeding rates were twice as high during a year in which the independently estimated abundance of their primary food (sandlance) was high, than during a year when it was low (Uttley *et al.*, 1996). Unlike the diets of murre chicks breeding at Witless Bay and at the Gannet Islands, those of chicks at Shetland did not vary between years. The fluctuations in feeding rates at Shetland probably resulted from the fact that sandlance were the birds' only available chick food (Kunzlik, 1989 in Uttley *et al.*, 1996; Monaghan *et al.*, 1996)

Both in Witless Bay and at Shetland, breeding murres spent more time foraging when prey availability was low (Burger and Piatt, 1990; Monaghan *et al.*, 1994; 1996). In conjunction with the fact that feeding rates at the Gannet Islands and in Witless Bay did not fluctuate with prey availability, this suggests that when alternative prey are available, murre

chick feeding rates are not primarily regulated by the availability of "preferred" prey, but rather by chick requirements. Thus, at the Gannet Islands, murres' feeding rates did not provide reliable information about food availability.

2.5.5 Chick growth

For the purposes of this study, conclusions about chick growth drawn from intercolony comparisons are necessarily dubious. This is because factors other than diet composition can effect growing chicks differently at different colonies. Such factors might include temperature, humidity and genetic constraints, although Gaston (1985) showed that between colony differences in temperature did not correspond to differences in fledge weights of Thick-billed Murres. Despite the possibility that diet alone does not determine chick growth rate, determining relative rates and magnitudes of chick growth can be informative (Tables 2.16 and 2.17).

Because Thick-billed Murres at the Gannet Islands in 1997 grew as well as or better than Thick-billeds at other colonies, and because the fledge weights of regularly handled chicks in 1997 were within two per cent of those of undisturbed chicks in 1983, I believe that that they grew at least as well in the nineties as they did in the eighties. In 1997 observers often saw Thick-billed Murre chicks refuse fish from their parents, which is consistent with the contention that they grew well.

Common Murre chicks from the Gannet Islands grew well in 1997 in comparison to those from other colonies, and their 1996 fledge weights were equivalent to those in 1981. Therefore, I have little reason to believe that the growth rates of Common Murre chicks differed before and after the decline in capelin availability.

2.5.6 Adult mass

Although the masses of Common and Thick-billed Murre adults were lower during chick rearing than during incubation, they were not lower in 1996/7 than they were in the 1980s during either period. Therefore, I found no evidence that the decrease in capelin abundance resulted in increased physical stress on breeding adult murres, or that adult mass correlates with capelin abundance.

Common Murres might be less adapted for searching for single fish among rocks on the sea floor than for preying upon schooling fish. The Common Murre's wing shape lends itself to agile maneuvering underwater, facilitating the speed and dexterity required to catch schooling fish (Spring, 1971). But Common Murres' pectoral muscles are smaller and less myoglobin-rich than Thick-billed Murres' (Spring, 1971), making it more difficult for the former to perform the deep or prolonged dives that might be necessary to catch demersal or crevice- dwelling fish (Croll *et al.*, 1992). Given these morphological and physiological constraints, it would be reasonable to suppose that a decrease in the body condition of Common Murres would be attendant upon switching from foraging for capelin to foraging for shannies. This did not happen at the Gannet Islands, where chick-rearing Common Murres' adult masses in 1996 and 1997 were similar to those in the 1980s.

I can imagine two reasons for the observed lack of body condition deterioration after Common Murres began foraging primarily for shannies. The first is that Common Murres did not expend more *effort* to catch a shanny than to catch a capelin - but they did take more *time* to do so. This is consistent with the observation that Common Murres' time-at-site was low during the years when they fed their chicks mostly shannies. Yet also consistent with this observation is the possibility that Common Murres' catch-per-unit-effort for shannies is, in fact, lower than it is for capelin, but adult body condition does not reflect this difference because when they feed their chicks shannies, murres spend more

time eating to make up for the energy spent foraging. These two possibilities could be distinguished only by the results of extensive time-activity budget and energy expenditure studies conducted both during years when murres feed their chicks capelin and during years when they feed their chicks shannies.

2.5.7 Time at site

Despite the fact that breeding murres spend a substantial portion of "free time" at sea (Cairns, *et al.* 1987; Benvenuti *et al.*, 1998), the amount of free time they spend on land seems to indicate the relative abundance of key species in the diets of their chicks. On Gull Island, Newfoundland, the amount of time off-duty Common Murres spent at their site decreased with the abundance of capelin near the island (Burger and Piatt, 1990). At the Shetland Islands, off-duty chick-rearing Common Murres increased their time-at site by five hundred percent after sandlance, their chicks' primary meal item, became more abundant near the colony (Monaghan *et al.*, 1996; Uttley *et al.*, 1994).

Although Cairns *et al.* (1987) showed that the proportion of time Common Murres spend diving decreases with the duration of their foraging trip Monaghan *et al.*. (1994) demonstrated that trip duration, hence time-at site, provides a reliable index of the foraging effort of murres. Using radiotelemetry to track the activities of breeding Common Murres away from the colony, they found that as foraging trip time increased (and time at site decreased) murres made more diving bouts per trip, performed more dives per bout, and paused for fewer seconds following dives of similar length than they did on shorter trips. Therefore, although time-at-site might not provide an absolute measure of Common Murres' free time, it can accurately gauge the proportion of time they allocate to foraging, which in turn reflects the availability of supposedly preferred prey items.

Data are not available to make between-year comparisons of Gannet Island murres' TAS. However, I can compare the TAS of Gannet Islands Common Murres' with those of Common Murres at other colonies and speculate about relative foraging efforts (Figure 2.7). Members of Common Murre pairs on Gull Island between 1983 and 1985 spent a mean of 22 per cent of daylight hours together (Burger and Piatt, 1990). Given their chicks' feeding rates, and assuming that foraging duty birds only visited their sites when delivering feeds, they spent a mean of 66 minutes together per visit. This figure probably exaggerates the birds' TAS, because foraging duty murres sometimes visit their sites in-between feeds (pers. obs.). Yet even if the true TAS of Gull Island Murres had been half of the projected 66 minutes, the birds would have spent well over twice as long together per visit than Gannet Islands Murres did. A more direct comparison reveals that Common Murres at the Gannet Islands in 1997 spent five times less TAS than Shetland Islands Common Murres did when sandlance were abundant (Monaghan *et al.*, 1996). But when sandlance were scarce, the TAS of Shetland Islands Murres was similar to those of the murres at the Gannet Islands. Thus, compared to those recorded at other colonies, Gannet Islands Murres' foraging effort, as measured by TAS, was very high. This suggests that at the Gannet Islands, Common Murres' TAS might correlate negatively with the local abundance of capelin. However, based on an analysis of brooding shift durations of Common Murres at the Gannet Islands in 1983, Verspoor *et al.* (1987) surmised that even in that year, off-duty murres spent little time at their sites. No measurements nor estimates were made of the murres' time spent together at the site in the 1980s. Without time-at-site data for years of varying capelin availability, the suggestion that Gannet Islands murres' time at site varies with capelin abundance remains provisional.

While Common Murre TAS seems to correspond to foraging effort, the link between Thick-billed Murre TAS and foraging effort is less obvious. This is because there

are few published data on Thick-billed murres' time-at-site in relation to changing prey availability or chick diets. Because Thick-billed Murres behave less gregariously toward their mates and chicks than Common Murres do (pers. obs. and see Birkhead, 1985), Thick-billeds might keep time-at site constant, increasing only free-time at sea as feeding conditions improve. Or, like Common Murres, they might adjust time-at site as feeding conditions change. The former possibility is more likely, because unlike Common Murres at the Gannet Islands, Thick-billed Murres tend to nest shoulder-to-shoulder on narrow cliff ledges, where adults often have difficulty sharing the small space available at their site. I have regularly seen foraging duty Thick-billed Murres balanced precariously on the edge of a ledge, flapping their wings in order to stay poised on the cliff long enough to feed their chick. These birds did not linger at their site after feeding.

During the year of higher sandlance availability at the Shetland Islands, Common Murres on the foraging shift made multiple foraging trips before taking up brooding duties, whereas during the poor year, they usually changed-over after each trip (Monaghan et al., 1996). I can not determine whether the murres at the Gannet Islands made multiple foraging trips per foraging shift. I have no data on how far the murres were foraging from the colony. These would be interesting, though, because Common Murres and shags breeding at the Shetland Islands foraged farther from the colony when sandlance were less abundant (Monaghan, 1996). Because I collected TAS data in only one year, and because the Gannet Islands murre population is not marked, I do not know whether increases in TAS are related to decreased life expectancy or fitness. If TAS does indeed fluctuate inversely with foraging effort, such decreases would be expected.

2.5.8 Conclusions

With respect to each of the parameters I measured, Common and Thick-billed Murres responded similarly to changes in capelin abundance. In keeping with the suggestions of Cairns *et al.* (1987), and the findings of other researchers (Burger and Piatt, 1990, Monaghan *et al.*, 1994, 1996; Uttley *et. al.* 1996) I observed that Common and Thick-billed Murres' productivity and feeding rates did not fluctuate in response to a decline in the abundance of capelin, an historically important item in their chicks' diets. Their chicks' diets changed substantially, however. Common Murres delivered significantly fewer capelin to their chicks, supplementing their diets with daubed shannies. This shift in foraging primarily for pelagic to benthic fauna is extremely rare for breeding Common Murres. Thick-billeds abandoned foraging for capelin, and almost solely fed their chicks daubed shannies. Such a diet is not as unusual for Thick-billed Murre chicks as it is for Common Murre chicks.

The rates of fish deliveries to murre chicks did not fluctuate consistently with the proportion of capelin in their diets. I can speculate with confidence that the growth of murre chicks was not affected by changes to their diet composition. Neither the masses of breeding adults nor their colony attendance responded negatively to this dietary shift. With the exception of chick diet composition, the amount of time pair members spend together during a chick feeding visit might be the only parameter that measurably changed in accordance with chick-diet variation. By the standards of Common Murres at other colonies (Burger and Piatt, 1990, Monaghan *et al.*, 1994), neither Common nor Thick-billed Murres at the Gannet Islands spent much time together at their sites while chick rearing. This suggests that their time spent foraging was high, supporting the hypotheses of Cairns *et al.* (1987) and Burger and Piatt (1990) that murres budget their time so as to buffer the

effects of prey availability. To exclude the possibility that the TAS of Gannet Islands murres is relatively low regardless of chick food abundance, more years of TAS and fish abundance data are necessary.

Table 2.1: Common Murre breeding success in 1981, 1982, 1983, 1996 and 1997. 1981-3 data from Birkhead and Nettleship, 1987b.

year	# eggs laid	# chicks hatched	hatching success (%)	# chicks fledged	fledging success (%)	breeding success (%)
1981	241	218	90.5	208	95.4	85.5
1982	248	203	81.9	193	95.1	77.9
1983	251	206	82.1	199	96.6	79.3
1996	139	118	84.9	116	98.3	83.5
1997	109	95	87.2	93	97.9	85.3

Table 2.2: Thick-billed Murre breeding success in 1981, 1982, 1983, 1996 and 1997. 1981-3 data from Birkhead and Nettleship, 1987b.

year	# eggs laid	# chicks hatched	hatching success (%)	# chicks fledged	fledging success (%)	breeding success (%)
1981	135	87	64.4	79	90.8	58.5
1982	153	108	70.6	95	88.0	62.1
1983	119	78	65.5	64	82.0	53.7
1996	144	105	72.9	102	97.1	70.8
1997	143	83	58.0	73	88.0	51.0

Table 2.3: Mean numbers of adult murres counted throughout the breeding season on plots Thick-billed A, Thick-billed C and Common C in 1981 and 1996. 1981-3 data from Birkhead and Nettleship, 1982.

plot-year	mean # birds/count	st. dev.	# of counts
Thick-billed A 1981	93	12	10
Thick-billed A 1996	194	37	61
Thick-billed C 1981	141	25	8
Thick-billed C 1996	140	35	61
Common C 1981	101	17	7
Common C 1996	121	21	61

Table 2.4: Common Murre chick diet composition in 1996. N is the number of feeds of the diet item in question delivered to chicks on plot Common-A during 10 1400-1800 feeding watches. Total mass of fish is estimated from the mean masses of each diet item collected from Common Murre parents. Other items include sandlance , Arctic cod, sculpin and squid. Unknown fish were those delivered to chicks before observers could identify their distinguishing features.

diet item	n	% by number	estimated total mass (g)	estimated % by mass
capelin	43	12	731	79
shanny	313	84	3193	18
other	17	4	136	3
total for known fish	373		4060	
unknown fish	24			

Table 2.5: Common Murre chick diet composition in 1997. N is the number of feeds of the diet item in question delivered to chicks on plot Common-A during 10 1400-1800 feeding watches. Total mass of fish is estimated from the mean masses of each diet item collected from Common Murre parents. Other items include sandlance , Arctic cod, sculpin and squid. Unknown fish were those delivered to chicks before observers could identify their distinguishing features.

diet item	n	% by number	estimated total mass (g)	estimated % by mass
capelin	170	45	2193	50
shanny	200	53	2120	48
other	10	2	80	2
total for known fish	380		4393	
unknown fish	24			

Table 2.6: Odds of capelin and shanny deliveries to Common Murre chicks. The odds of a delivery equals the number deliveries of that fish observed during four hour feeding watches divided by the number of deliveries of other fish.

year	odds of capelin delivery	odds of shanny delivery	n
1982	3.2	0.10	2085
1983	3.1	0.18	1640
1996	0.14	5.0	364
1997	0.81	1.1	380

Table 2.7: Between-year ratios of the odds of capelin and blenny deliveries to Common Murre chicks. 'Ratio capelin/blenny delivery' is the ratio of the natural log of the odds of a delivery of the fish in the first year in year pair to that in the second year in year pair. 'c.l.' is the 95 per cent confidence interval of the ratio of the log of the odds.

year pair	ratio capelin delivery	c.l. capelin delivery	**year pair**	ratio blenny delivery	c.l. blenny delivery
82:96	3.14	2.80-3.47	**82:96**	-3.89	-4.20 - -3.57
82:97	1.37	1.15-1.60	**82:97**	-3.20	-3.50 - -2.90
83:96	3.01	2.76-3.43	**83:96**	-3.32	-3.36 - -3.02
83:97	1.33	1.10-1.56	**83:97**	-2.64	-2.93 - -2.34
96:97	-1.76	-1.39 - -2.14	**96:97**	0.69	0.31 - 1.06

Table 2.8: Thick-billed Murre chick diet composition in 1996. N is the number of feeds of the diet item in question delivered to chicks on plot Thick-billed A during 8 1400-1800 feeding watches. Total mass of fish is estimated from the mean masses of each diet item collected from Common Murre parents. Unknown fish were those delivered to chicks before observers could identify their distinguishing features.

diet item	n	% by number	estimated total mass (g)	estimated % by mass
capelin	2	2	34	3
shanny	107	97	1070	96
other	1	1	8	1
total for known fish	110		1112	
unknown fish	125			

Table 2.9: Thick-billed Murre chick diet composition in 1997. N is the number of feeds of the diet item in question delivered to chicks on plot Thick-billed A during 10 1400-1800 feeding watches. Total mass of fish is estimated from the mean masses of each diet item collected from Common Murre parents. Unknown fish were those delivered to chicks before observers could identify their distinguishing features.

diet item	n	% by number	estimated total mass (g)	estimated % by mass
capelin	9	6	116	7
shanny	139	94	1473	93
other	0	0	0	0
total for known fish	148		1589	
unknown fish	241			

Table 2.10: Odds of capelin and shanny deliveries to Thick-billed Murre chicks. The odds of a delivery equals the number deliveries of that fish observed during four hour feeding watches divided by the number of deliveries of other fish.

year	odds of capelin delivery	odds of shanny delivery	n
1982	0.24	2.6	241
1983	0.43	2.0	409
1996	0.02	35.7	110
1997	0.06	12.6	151

Table 2.11: Between-year ratios of the odds of capelin and blenny deliveries to Thick-billed Murre chicks. 'Ratio capelin/blenny delivery' is the ratio of the natural log of the odds of a delivery of the fish in the first year in year pair to that in the second year in year pair. 'c.l.' is the 95 per cent confidence interval of the ratio of the log of the odds.

year pair	ratio capelin delivery	c.l. capelin delivery	**year pair**	ratio blenny delivery	c.l. blenny delivery
82:96	2.36	1.07 - 3.65	**82:96**	-2.47	-3.58 - -1.37
82:97	2.93	1.66 - 4.20	**82:97**	-2.75	-3.84 - -1.67
83:96	1.13	0.58 - 2.04	**83:96**	-1.55	-2.21 - -0.88
83:97	1.88	1.19 - 2.57	**83:97**	-1.82	-2.46 - -1.19
96:97	-1.05	-2.46 - 0.39	**96:97**	0.93	-0.29 - 2.15

Table 2.12 Common Murre chick diet composition in 1982. N is the number of feeds of the diet item in question delivered to chicks during four-hour and all-day feeding watches, as well as fish caught from parents. Total mass of fish is estimated from the mean masses of each diet item collected from Common Murre parents. Other items include sandlance, fish doctor, Atlantic and Arctic Cod and sculpin. Unknown fish were those delivered to chicks before observers could identify their distinguishing features. Data from Birkhead and Nettleship, 1987a.

diet item	n	% by number	estimated % by mass
capelin	1589	82	78
shanny	198	12	10
other	298	6	12
total	2085		

Table 2.13 Common Murre chick diet composition in 1983. N is the number of feeds of the diet item in question delivered to chicks during four-hour and all-day feeding watches, as well as fish caught from parents. Total mass of fish is estimated from the mean masses of each diet item collected from Common Murre parents. Other items include sandlance, fish doctor, Atlantic and Arctic Cod and sculpin, fourline snakeblenny, eelpout and flatfish. Data from Birkhead and Nettleship, 1987a.

diet item	n	% by number	estimated % by mass
capelin	1237	75	80
shanny	257	16	12
other	154	9	8
total	1648		

Table 2.14: Thick-billed Murre chick diet composition in 1982. N is the number of feeds of the diet item in question delivered to chicks during four-hour and all-day feeding watches, as well as fish caught from parents. Total mass of fish is estimated from the mean masses of each diet item collected from Common and Thick-billed Murre parents. Other items include sandlance and gadids. Data from Birkhead and Nettleship, 1987a.

diet item	n	% by number	estimated % by mass
capelin	174	72	71
shanny	47	20	22
other	20	8	7
total	241		

Table 2.15: Thick-billed Murre chick diet composition in 1983. N is the number of feeds of the diet item in question delivered to chicks during four-hour and all-day feeding watches, as well as fish caught from parents. Total mass of fish is estimated from the mean masses of each diet item collected from Common and Thick-billed Murre parents. Other items include sandlance, fish doctor, gadids and fourline snakeblenny. Data from Birkhead and Nettleship, 1987a.

diet item	n	% by number	estimated % by mass
capelin	271	66	61
shanny	123	30	36
other	15	4	3
total	409		

Table 2.16: Growth of regularly weighed Common Murre chicks at various colonies in different years, listed in descending order of maximum growth rate. 'Mid point weight' is the median of hatch weight and fledge weight. Gull Island data from Mahoney, 1976; Farne Island data from Pearson, 1968; Skomer Island data from Birkhead, 1976, in Gaston, 1985a; Stora Karlso data from Hedgren and Linnman, 1979. Most data compiled by Gaston (1985a).

colony	max growth rate (g/day)	mid point weight (g)	fledge weight (g)	fledge weight (per cent adult mass)
Stora Karlso, 1975	15.7	160	239	—
Stora Karlso, 1974	15.5	165	266	—
Gannet Islands, 1997	15.2	148	233	25
Gull Island, 1978	14.2	167	260	26
Gull Island, 1977	14.1	167	216	22
Gannet Islands, 1981	13.8	140	246	26
Stora Karlso 1977	13.1	165	242	—
Farne Island, 1965	12.6	152	250	27
Stora Karlso, 1976	12.3	160	240	—
Skomer Island, 1974	11.8	142	215	25

Table 2.17: Growth of regularly weighed Thick-billed Murre chicks at various colonies in different years, listed in descending order of maximum growth rate. 'Mid point weight' is the median of hatch weight and fledge weight. Cape Hay and Coburg Island data from Birkhead and Nettleship, 1981; Prince Leopold Island data from Gaston and Nettleship, 1981. Most data compiled by Gaston (1985a).

colony	max growth rate (g/day)	mid point weight (g)	fledge weight (g)	fledge weight (% adult mass)
Gannet Islands, 1997	15.2	150	224	24
Prince Leopold Island, 1975	14.4	136	204	23
Coburg Island, 1979	13.0	146	206	24
Prince Leopold Island, 1977	11.6	149	221	25
Cape Hay, 1979	11.4	135	191	22
Prince Leopold Island, 1976	8.5	144	212	24
Digges Island, 1980	8.4	110	157	17
Digges Island, 1980	6.8	105	146	15

Table 2.18: Mean masses of incubating and chick-rearing Common Murres in 1981, 1982, 1983, 1996 and 1997. 1981-1983 data from Birkhead and Nettleship, 1987a.

year	mean mass incubation (g)	st. dev.	n	mean mass chick-rearing (g)	st. dev.	n
1981	980	61	30	909	64	24
1982	993	61	31	944	56	30
1983	975	56	31	960	50	30
1996	---			945	66	106
1997	1011	64	13	960	74	64

Table 2.19 : Mean masses of incubating and chick-rearing Thick-billed Murres in 1981, 1982, 1983, 1996 and 1997. 1981-1983 data from Birkhead and Nettleship, 1987a.

year	mean mass incubation (g)	st. dev.	n	mean mass chick-rearing (g)	st. dev.	n
1981	943	51	30	899	57	30
1982	971	68	30	903	47	20
1983	955	58	20	---		
1996	945	64	71	900	68	46
1997	943	65	23	919	59	11

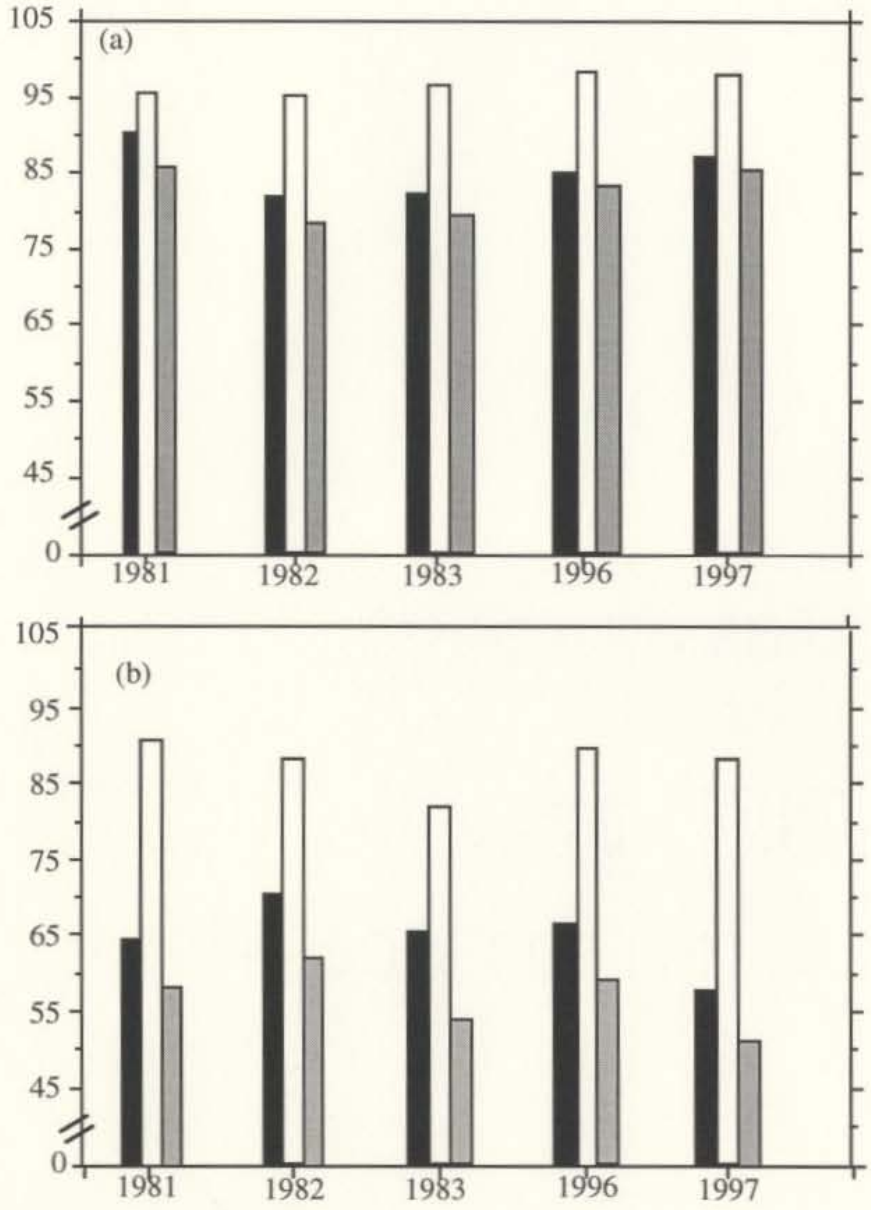

fig.2.1: Percent of eggs laid that hatched (black bars), chicks hatched that fledged (white bars) and eggs laid at sites from which chicks fledged (grey bars) for Common Murres (a) and Thick-billed Murres (b) on productivity plots on in 1981, 1982, 1983, 1996 and 1997. 1981-1983 data from Birkhead and Nettleship, 1987b.

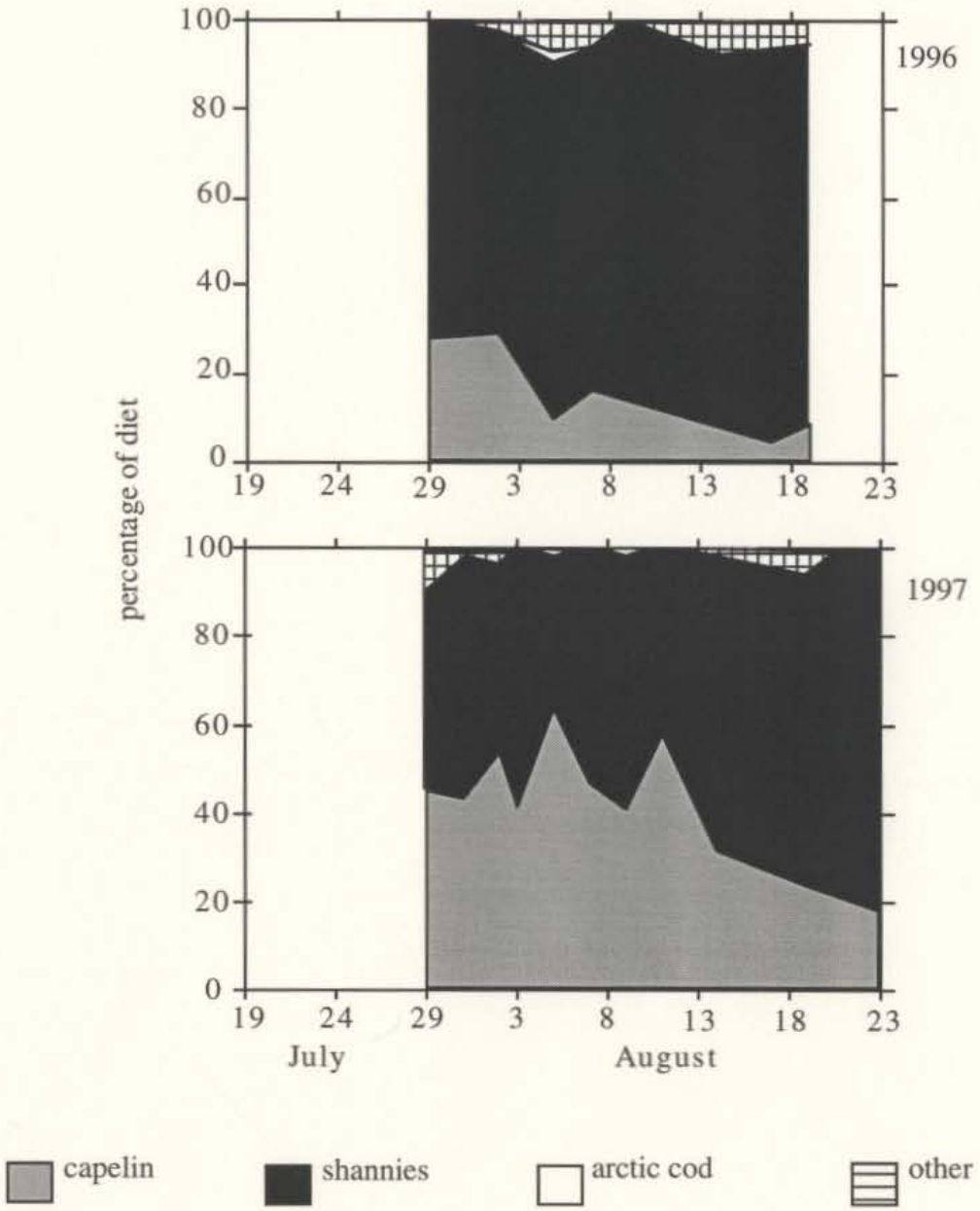

fig 2.2: Percentages by number of capelin, shannies, arctic cod and other fish in diets of Common Murre chicks in 1996 and 1997.

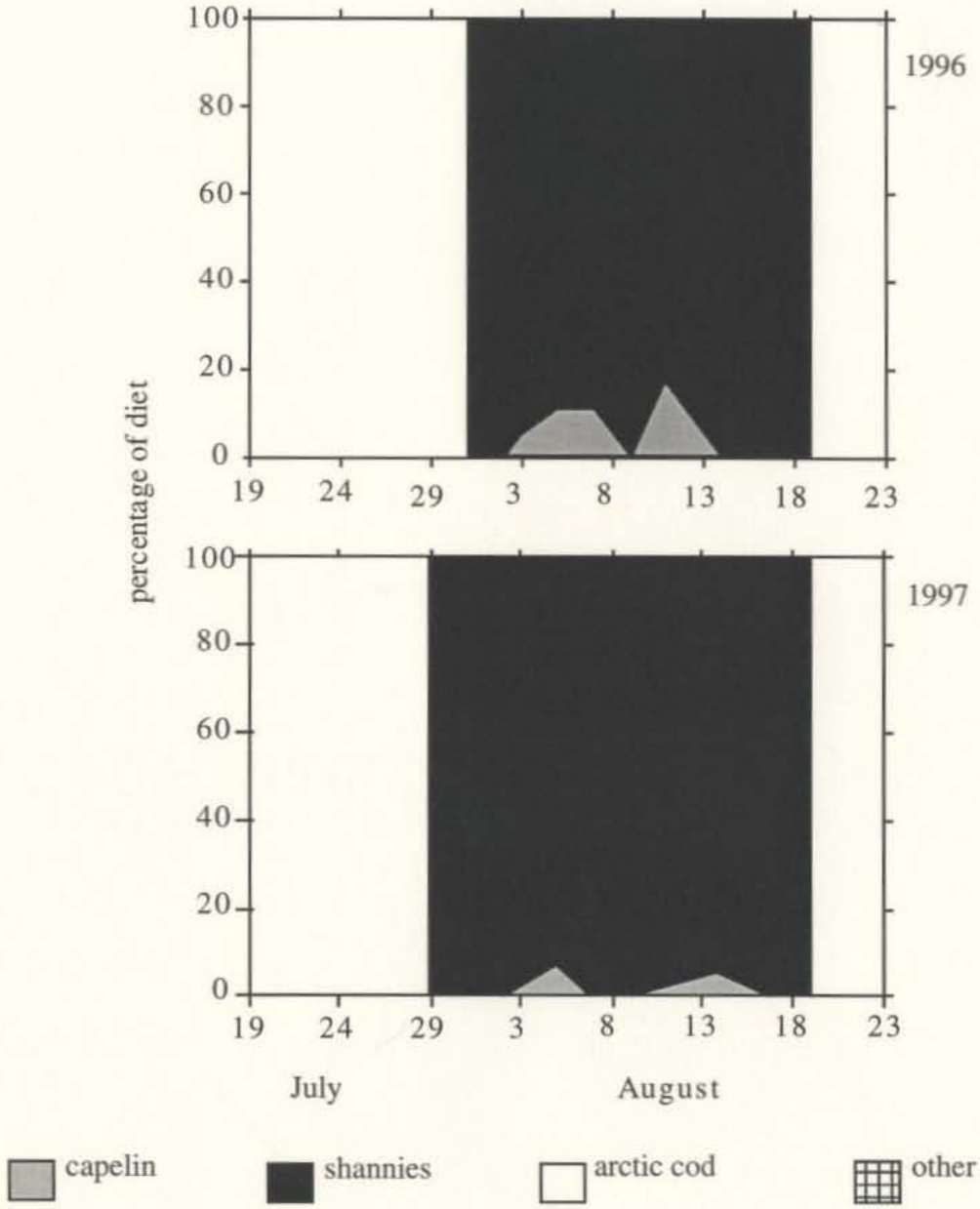

fig 2.3: Percentages by number of capelin, shannies, arctic cod and other fish in diets of Thick-billed Murre chicks in 1996 and 1997.

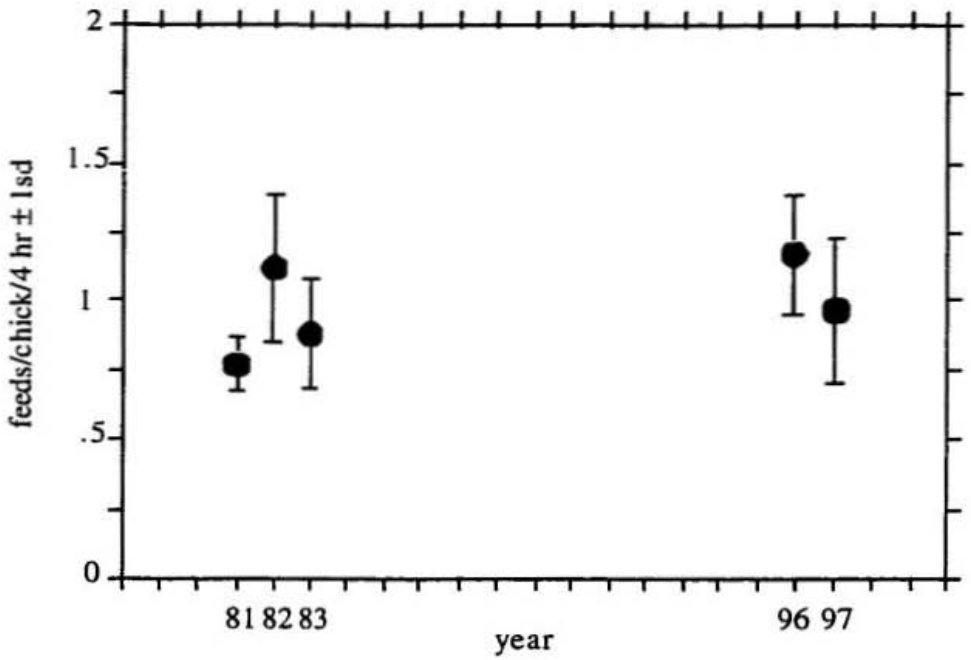

fig 2.4: Mean rates of fish deliveries to Common Murre chicks between 1400h and 1800h in 1981 (n=8 feeding watches), 1982 (n=11), 1983 (n=12), 1996 (n=8) and 1997 (n=11). 1981-83 data from Birkhead and Nettleship (1982, 1985).

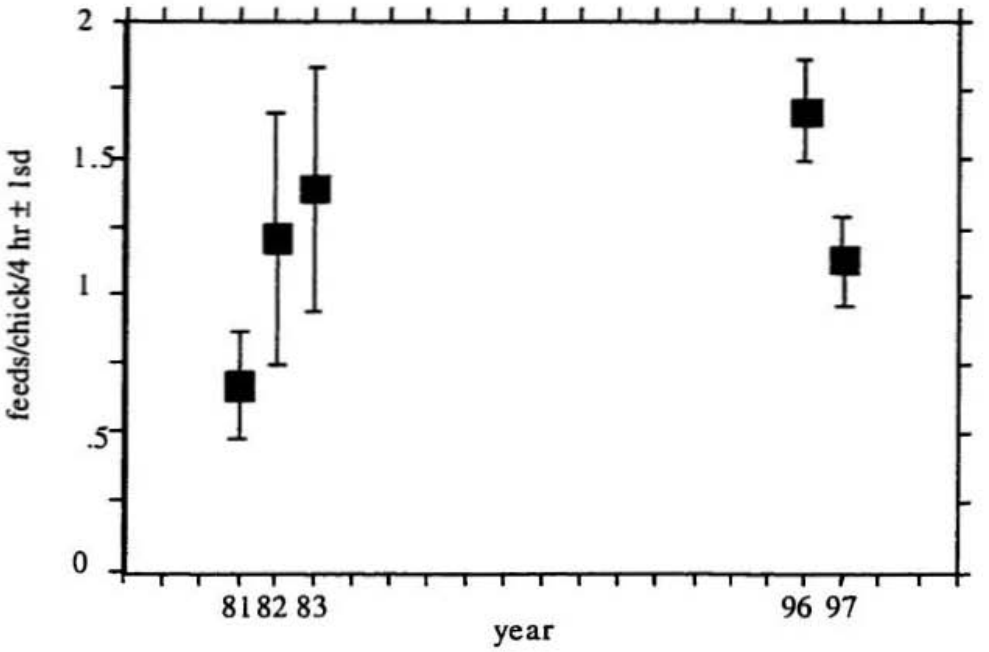

fig 2.5: Mean rates of fish deliveries to Thick-billed Murre chicks between 1400h and 1800h in 1981 (n= 12 feeding watches), 1982 (n=11), 1983 (n=12), 1996 (n=8) and 1997 (n=9). 1981-83 data from Birkhead and Nettleship (1982,1985).

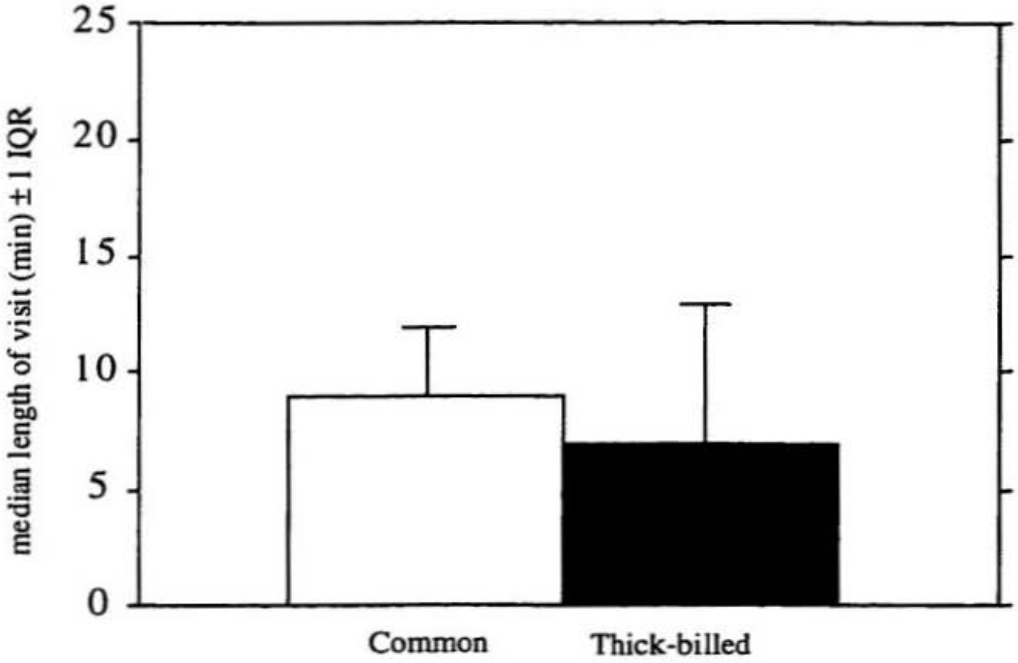

figure 2.6: Median numbers of minutes (+ interquartile ranges) Common and Thick-billed Murre pair members spent together per feeding visit during the chick rearing period in 1997.

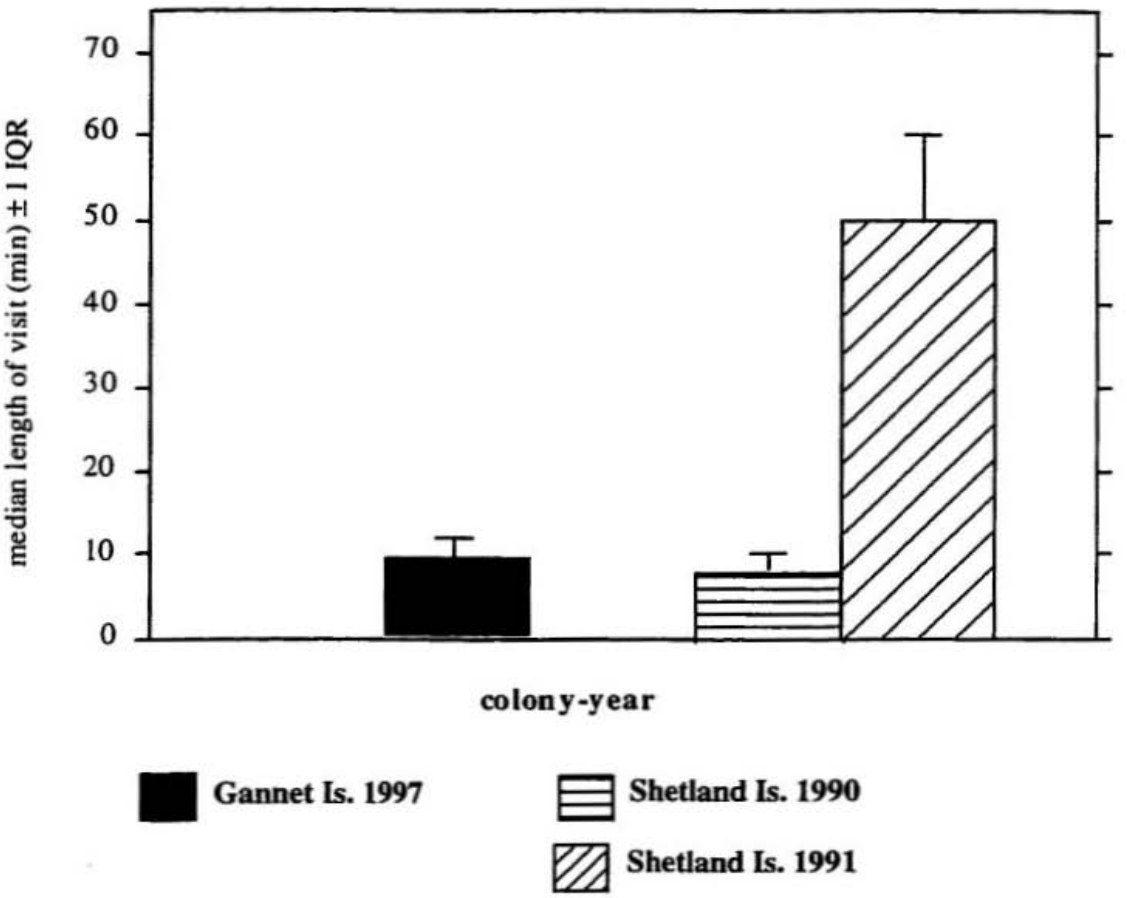

figure 2.7: Median numbers of minutes (+ interquartile ranges) Common Murre pair members spent together per feeding visit during the chick rearing period. Shetland Islands data from Monaghan *et al.*, 1996.

CHAPTER 3

FOOD RESOURCE USE BY COMMON AND THICK-BILLED MURRES BREEDING AT THE GANNET ISLANDS

3.1 ABSTRACT

I used Monte Carlo randomization to establish whether Common and Thick-billed Murre chick diet diversity, food niche breadth and diet overlap in two years were greater than would be expected by chance. Diet diversity and niche breadth were uniformly lower than predicted by the null model. Diet overlap was higher than 75 per cent in both years, but was higher than predicted by the null model only in one year, when capelin were less prevalent in the diets. To determine whether the two murre species' chick food resource use converged along axes other than diet composition, I compared timing of breeding in two years, and in one year I compared timing of breeding, sizes of fish delivered to chicks, maximum dive depths and diurnal feeding patterns of breeding Common and Thick-billed Murres. In both years, the murres' chick rearing periods overlapped almost exactly. In the year they were measured, the sizes of the principal item in their chicks' diets did not differ significantly. During one of two all- day feeding watches in one year, the murres' chick-feeding peaks were concurrent, but during the other they were not. In the year dive depths of both species were measured, Common and Thick-billed Murres dove to similar maximum depths. In combination, these results suggest that chick food resource partitioning might have been negligible between Common and Thick-billed Murres at the Gannet Islands.

3.2 INTRODUCTION

Gause's Law - or the competitive exclusion principle - states that in sympatry, species that are closely related will differentiate ecologically (Gause, 1934). A testable hypothesis derived from the principle would be: sympatric species that are similar along one niche dimension will differ along another, effectively diminishing resource use overlap (niche complementarity hypothesis, Schoener, 1974).

This hypothesis has been supported by many studies, including Cody's (1974) work on grassland bird communities, Lack's (1947) studies of Darwin's finches and by the results of Schoener's (1968, 1970) research on lizards in Jamaica. However, not all research has championed the niche complementarity hypothesis. Barrett and Furness' work on the chick diet of Common and Thick-billed Murres in the Barents Sea offered only ambivalent support for the hypothesis (Furness and Barrett, 1985; Barrett and Furness, 1990; Barrett *et al.*, 1997). Barrett *et al.* (1997) reported high degrees of chick diet overlap, nearly identical maximum dive depths and foraging ranges, as well as similar patterns of diurnal feeds to chicks of both murre species. Although the birds' chick-rearing periods overlapped to an extent, Common Murres' median hatch date was earlier than Thick-billed Murres' and during some months, breeding Common Murres dove to shallower maximum depths than Thick-billed Murres.

Like the Barents Sea colonies, the Gannet Islands Ecological Reserve in the Labrador Sea is one of the only places in the Atlantic where the congeneric Common and Thick-billed Murres breed syntopically in high numbers (Nettleship and Evans, 1985). At the Gannets, Murres could segregate their chick-provisioning effort in at least six ways:

1. by breeding at different times
2. by taking different fish species

3. by taking different sizes or sexes of fish

4. by foraging from different locations on the sea surface

5. by foraging at different depths

6. by foraging during different times of day

I investigated possibilities 1, 2, 3, 5, and to some extent 6 by determining the timing of Common and Thick-billed Murre chick rearing periods and by measuring chick diet diversity, niche breadth and overlap; the sizes and sexes of prey delivered to chicks; the maximum dive depths of brooding birds; as well as by determining the diurnal pattern of feeds to chicks during the 1996 and 1997 breeding seasons. I used Monte Carlo randomizations to determine the significance of observed diversity, niche breadth and overlap values.

3.3 METHODS

3.3.1 Timing of breeding

To determine the timing of Common and Thick-billed Murres' chick rearing periods, Mark Hipfner and I recorded the hatch and fledge dates of chicks on the productivity plots in 1996 and 1997 (Common 1996 n= 180, 1997 n= 140; Thick-billed 1996 and 1997 n=150). The methods I used to establish hatch and fledge dates are described in Chapter 2. In calculating median hatch dates (MHDs), I used only hatch dates of which I was certain to within 24-hours.

3.3.2 Niche breadth, diet diversity and diet overlap

To establish the murre chick diet composition used to calculate niche breadth, diet diversity and diet overlap, I conducted feeding watches with the help of observers. In 1996 we conducted eight Common and eight Thick-billed Murre four-hour feeding watches. In 1997 we conducted 11 Common and nine Thick-billed Murre four-hour feeding watches.

Please refer to Chapter 2 for a detailed description of how chick diet was recorded and described .

I used Levins' (1968) standardized index to determine Common and Thick-billed Murres' niche breadth as it related to chick diet. Levins' formula calculates niche breadth as:

$$\frac{1/(\Sigma\, p_i^{\,2})-1}{n-1}$$

where p_i is the proportion of item i in the chicks' diets. To characterize the diversity of murre chick diets, I used the Shannon-Weaver H' . This index describes diversity as:

$$-\Sigma p_i\, (\ln\, p_i)$$

where p_i is the proportion of item i in the chicks' diets. As recommended by Wolda (1981), I used Horn's (1966) adaptation of Morisita's (1959) index of resource use overlap to characterize the similarity of Common and Thick-billed Murre chick diets. This index calculates diet similarity as:

$$\frac{2\,\Sigma x_i y_i}{\Sigma\, x_i^{\,2} + \Sigma\, y_i^{\,2}}$$

Where X_i is the proportion of X's diet accounted for by item i . The niche breadth and diet overlap indices are standardized and range from 0 to 1, whereas the Shannon-Weaver H' is not standardized.

The proportions of each item used in the above indices are derived from percentages by number of the items in the murre chicks' diets. Because each chick meal consisted of a single fish, and because the sizes of these fish do not vary much, percentage by number approximates percentage by mass (see Chapter two).

I considered a diet item to be the lowest taxon to which I could identify a meal from the blind (Table 3.1). Hence, most items comprised species of fish while others comprised genera or families. Although this taxonomy is rather arbitrary, it loosely reflects fishes' behaviour and arguably converges on murres' discrimination between items. I did not segregate species by size or sex when creating diet item categories. This is because the sizes of items did not vary much and for the items I sexed, there was virtually no variation in sex.

I used Monte Carlo randomization to ascertain whether the murres' chick diet diversities, niche breadths and diet overlap differed significantly from those calculated from randomly generated diets. Randomization minimizes the type II errors that typify interpretations of observed values of these indices, affording a less capricious assessment of the significance of patterns of resource use. For each parameter in this case, 5000 randomizations were performed because with fewer randomizations, the variance around p values obtained from behavioural data can be undesirably high (Adams and Anthony, 1996). For each murre species in each year, I created 5000 randomly construed diets. Each of these diets consisted of the same number of feeds observed in that year and composed of the same diet items I recorded during feeding watches. For instance, during four-hour watches in 1997 I observed 404 Common Murre chick feeds, each of which consisted of either capelin, shanny, gadid, sandlance, sculpin or squid. Therefore, I generated a group of 405 feeds 5000 times, each feed consisting of a randomly selected member of the above listed set of diet items. From the 5000 randomly generated diets for year each, I calculated 5000 diet diversities and niche breadths for each murre species. Then, from the random distributions of each index I calculated the proportion of values that were more extreme than those I observed.

The set of items used for randomization of Thick-billed Murre chick diets was larger than the set of items they actually delivered to their chicks in each year. This is

because I assumed that any item fed by one species of murre during either year of the study *and* fed by the other during the year in question was available to both during the year in question. Thus, I included items in the Thick-billed Murres randomized diets if the Thick-billeds had delivered them in another year and if Common Murres delivered them during the year in question. For example, I included gadids in the set of items included in the 1996 Thick-billed randomized diet, because although Thick-billed Murres were not observed feeding gadids to their chicks in that year, they were observed delivering gadids in 1997 *and* Common Murres were observed delivering gadids in 1996.

From the 5000 randomly generated Common and Thick-billed murre diets for each year, I calculated 5000 chick diet overlap scores. As for diversity and niche breadth, I found p values for the observed diet overlaps by calculating the proportion of values in the random distribution that were more extreme than those observed.

3.3.3 Size, sex and reproductive state of fish delivered to chicks

At regular intervals during the chick-rearing period in 1996 and 1997, I collected chick diet samples from Common Murres in. These were collected from parents as they returned to their sites from the sea. Wielding a dip-net-like fleyge, I caught or startled Common Murres flying with fish in their bills. This caused the birds to drop their fish, which I then collected. In 1997, other researchers collected Thick-billed Murres chick diet samples from ledges on which breeding birds held sites. No diet samples were collected from birds nesting on or near productivity or feeding watch plots.

Intact fish collected both directly from birds and from ledges were weighed with an electronic balance to the nearest gram and their length measured to the nearest millimetre. The fork length of fish with forked tails (such as sandlance and capelin) was taken along with their total length. I measured 170 Common Murre chick meals in 1996. 124 of these were daubed shannies and 20 of them were capelin. In 1997 I measured 124 Common

Murre chick meals, 59 of which consisted of daubed shannies and 45 consisted of capelin. In 1997 I measured 28 Thick-billed Murre chick meals, all of which were daubed shannies.

In 1997, I examined the reproductive states of fish delivered to murre chicks. I determined whether a fish was gravid by squeezing it near the vent, or by making an incision there. If eggs oozed out of the vent, or if eggs were present in the fish's ovaries or body cavity, I determined it to be gravid. I sexed non gravid capelin by examining their color, the sizes of their anal fins and the texture of their dorso-lateral ridges. Capelin with prominent anal fins and raised dorso-lateral ridges I concluded to be male. Those with pinkish scales and small anal fins I concluded to be female. I established the sex of daubed shannies based on whether the fish had ovaries or testes. I examined the reproductive state of 51 daubed shannies fed to Common Murre chicks and 24 fed to Thick-billed Murre chicks.

I used two-tailed, unpaired t-tests to compare the mean masses and lengths of daubed shannies delivered to Common Murre chicks with those delivered to Thick-billed Murre chicks. I used ANOVAs to determine whether the mean masses and lengths of daubed shannies delivered to Common Murre chicks varied significantly between years. To compare the ratios of gravid and not gravid daubed shannies delivered to Common with those delivered to Thick-billed Murre chicks, I used a Chi square test of homogeneity. To compare the proportions of male to female capelin delivered to Common Murre chicks, as well as the proportions of gravid to not gravid female capelin, I used Chi square tests of independence.

3.3.4 Diurnal feeding patterns

In addition to four-hour watches, with the help of other researchers I conducted feeding watches that included all daylight hours. These lasted 16-17 hours, from

approximately 0430h until 2130h. Four Common Murre all-day watches were done in 1996 (on August 4, 9, 16 and 21) and four were done in 1997 (On August 5, 9, 11 and 21). Two Thick-billed all-day watches were done in 1997 (these were simultaneous with the August 5 and 11 Common Murre all-day watches). During all-day watches observers' shifts in the blind never exceeded 4-hours.

To determine whether the frequency of feeds delivered during these four periods varied for or differed between Common and Thick-billed Murre chicks, I performed Chi-square analyses.

3.3.5 Maximum dive depths

In order to estimate the portion of the water column exploited by breeding murres, I measured the birds' maximum dive depths. I used noose poles to lift birds away from their sites prior to deploying or retrieving a depth gauge. In 1996, I deployed 74 capillary-tube maximum depth gauges (MDGs); (Burger and Wilson, 1988) on brooding and incubating Thick-billed Murres. In 1997 I deployed 19 MDGs on Thick-billed Murres and 14 MDGs on Common Murres. The gauges were retrieved within 48 hours in 1996 and within 24 hours in 1997. I only gauged birds of whose reproductive status (egg or chick) I was certain. No birds were caught on the plots monitored for productivity or chick diet. No birds were gauged more than once. I interpreted the depth gauge readings following Burger and Wilson (1988).

3.4 RESULTS

3.4.1 Timing of breeding

For the birds of whose hatch and fledge dates I was certain, the chick rearing periods of Common and Thick-billed Murres were highly synchronous in both 1996 and 1997 (Figures 3.1 and 3.2). In 1996, the Common Murres' chick-rearing period began on

July 20 and lasted until September 1. The Thick-billeds reared chicks between July 21 and September 5. The median hatch date (MHD) of chicks reared on the productivity plots was July 29 - the same for both species. The median hatch dates of those birds reared on the feeding plots differed only slightly between species; Common Murres' MHD was July 30 and Thick-billed Murres' MHD was July 31. In 1997, The Common Murres' chick-rearing period spanned from July 22 until September 3. The Thick-billeds' spanned from July 22 until August 26. July 31 was the MHD of the Common Murres and July 30 the MHD of Thick billed Murres reared on the productivity plots. On the feeding plots, the Common Murres' MHD was July 30, and the Thick-billeds Murres' was July 31.

3.4.2 Niche breadth, diet diversity and diet overlap

Shannies comprised the bulk of Common and Thick-billed Murre chick diets in 1996 and 1997. In both years, however, Thick-billeds seemed more reliant than Common Murres on shannies (Table 3.1). In addition to shannies, capelin accounted for a sizable proportion of Common Murre chick diets in both years. Other items in the chicks' diets included sandlance, sculpins, fish doctors, gadids and squid. Please refer to Table 3.1 and to Chapter two for a detailed description of chick diets.

Both Common and Thick-billed Murres' niche breadths in 1996 (0.079 and 0.009 respectively) were significantly lower than would be predicted were they random (Table 3.1, Figures 3.3 and 3.4). The mean niche breadths calculated from randomly generated diets fell between 0.97 and 0.99. All of the 5000 randomly generated niche breadths for each species were higher than the observed values. Thus, the p values for the observed niche breadths were less than 0.001. This held for the murres' 1997 niche breadths, as well. Common Murres' 0.221 and Thick-billed Murres' 0.37 were lower than any of those generated randomly.

Like their niche breadths, the murres' diet diversities were significantly lower than would be expected if the birds fed their chicks random proportions of each item in their diets (Table 3.1, Figures 3. 5 and 3.6). Common Murres' observed chick diet diversity in 1996 was 0.55 and in 1997 it was 0.82. The diversity of Thick-billed Murre chick diet in 1996 was 0.13 and in 1997 it was 0.27. The mean diversities of randomly generated chick diets were all above 2.30. The p values corresponding to each of the observed diversities were less than 0.001.

In 1996, Common and Thick-billed Murre chick diets were virtually identical (Table 3.1). The observed overlap in that year was 0.982. The mean of the 5000 overlaps calculated from randomly generated chick diets was 0.896. The 95% confidence limits around this mean were tight (0.850-0.935), hence the p value corresponding to the observed overlap was less than 0.001 (Figure 3.7).

The chick diets were less similar in 1997 than they were the previous year. Their overlap of 0.769 was similar to that which would be expected due to chance alone. The mean overlap of those calculated from randomly generated chick diets was 0.791. The observed value fell well within the 95% confidence limits of this mean (0.733-0.845); its p value was 0.788 (Figure 3.7).

3.4.3 Size, sex and reproductive state of fish delivered to chicks

In 1997, Common and Thick-billed Murres did not partition their resource exploitation by delivering their chicks differently-sized daubed shannies (Figure 3.8). Both the masses and the total lengths of daubed shannies fed to Common and Thick-billed chicks were similar (mass t=1.002, df=74, p=0.319; length t=1.214, df=83, p=0.23).

The mean mass of daubed shannies delivered to Common murre chicks in 1996 was 10.2± 1.6 g, and in 1997 it was 10.6+/- 2 g. These means did not differ significantly (t= -1.14, df= 176, p= 0.16). Likewise, the interyear difference between mean total

lengths of the daubed shannies was not significant (t= 0.186, df=181, p= 0.85). In 1996, the daubed shannies Common Murres fed their chicks had a mean length of 152±10mm and in 1997 they had a mean length of 151+/-11mm.

In 1997 I examined the reproductive state of 51 daubed shannies delivered to Common Murre chicks. Of these, 44 were gravid. Of the remaining seven, 4 were males and 3 were of unknown sex but were not gravid. Of of the 24 daubed shannies delivered to Thick-billed murre chicks, 17 were gravid. The seven fish that were not gravid included one male and six fish of unknown sex. The difference between Common and Thick-billed Murres' ratios of gravid to not gravid daubed shannies was not significant ($X^2 = 2.6$, df=2, p=0.30).

Common Murres fed their chicks larger capelin in 1996 (17 +/-4 g, 144+/-10 mm) than in 1997 (12.9 +/- 3.5 g, 135 +/- 11mm) (Figure 3.9). In 1996 the capelins' mean mass was 30 per cent higher (t= 2.5, df=63, p=0.0001) and their mean fork length was six per cent longer (t= 3.1, df=60, p=0.003).

In 1997 I determined the sex of 49 capelin brought to Common Murre chicks. Of these, 48 were female and one was male. This difference between the frequencies of males and females was significant ($X^2 = 45.1$, df=1, p=.0001). I ascertained the reproductive state of 42 of the female capelin. One was gravid and 41 were not. The difference between the frequencies of gravid and non-gravid capelin was significant ($X^2 = 38$, df=1, p= 0.0001). Of the females that were not gravid, seven had a few eggs in their body cavities, which suggests that they had already spawned.

3.4.4 Diurnal feeding patterns

When analyzed at a one hour scale, Common Murre chicks' feeding rates varied with time of day for three of four all-day feeding watches in 1996 and three of four feeding

watches in 1997 (X^2 tests of homogeneity, criterion of significance = 0.05; Figures 3.10, 3.11, 3.12, 3.13 and 3.14). The rates at which they were fed daubed shannies varied significantly with time of day during one all-day feeding watch in 1996 and two in 1997 (X^2 tests of homogeneity, criterion of significance = 0.05). Feeding rates to Thick-billed Murre chicks varied significantly with time of day during one of two all-day feeding watches in 1997 (X^2 tests of homogeneity , criterion of significance = 0.05; Figures 3.13 and 3.14). When fish deliveries varied with time of day, there were high early morning peaks and lower evening peaks in feeding rates to both Common and Thick-billed Murre chicks.

The hourly frequencies of feeds to Thick-billed Murre chicks did not differ significantly from the frequency of feeds delivered to Common Murre chicks during one of two simultaneous all day feeding watches in 1997 (August 5 watch X^2 = 8.81, df= 16, p= 0.9; August 11 watch X^2 = 26.6, df=16, p=0.05; Figures 3.13 and 3.14). The lack of significant difference between the murres' feeding patterns held when the frequencies of feeds were compared at one- two - three- and four-hour scales, but p values were highest at the one- hour scale (X^2 August 5 watch, 2 hr scale = 4.77, df=7, p=0.7; 3 hr scale X^2 = 3.53, df=5 p= 0.6; 4 hr scale X^2 = 3.51, df=3, p= 0.3). During the other simultaneous all day feeding watch, Common and Thick-billed Murres displayed different feeding patterns when those patterns were compared at all scales (X^2 august 11 watch, 2hr scale X^2 = 17.5, df=7, p=0.01; 3 hr scale X^2= 19.3, df=5, p=0.02; 4 hr scale X^2= 12.4, df= 3, p=0.006).

3.4.5 Maximum dive depths

Of the 40 incubating Thick-billed Murres outfitted with depth gauges in 1996, 25 were recaptured. Sixteen of them still bore readable gauges at the time of recapture. 32 chick rearing Thick-billed Murres were depth gauged in 1996, and 18 were recaptured.

Eleven of these still bore readable gauges. The mean maximum dive depths of incubating and brooding Thick-billed Murres did not differ significantly in 1996 ($t=0.907$, $df=25$, $p=0.373$). In 1997, I recaptured 7 of the nineteen chick rearing Thick-billed Murres that were depth gauged. All of their gauges were readable. The mean maximum dive depth of Thick-billed Murres in 1997 was not significantly different from that in 1996 ($t=0.589$, $df=32$, $p=0.560$). Of the 14 depth gauges I deployed on Common Murres in 1997, I retrieved only two. The depths they recorded (85m and 158m) were near the high and low limits of the range of Thick-billed Murre depths (40m-178m) (Figure 3.15).

3.5 DISCUSSION

3.5.1 Niche breadth and diet diversity

The extremely low niche breadths and diet diversities exhibited by both murre species in both years of the study result from the birds feeding disproportionate amounts of each diet item to their chicks. Yet the uncertainty of the relative availabilities of the murres' prey compromises the precision of my estimates of niche breadth. Levins' (1968) index ascribes the highest niche breadth values to diets comprised of equal proportions of each item therein. However, true generalist feeders take diet items in the proportions in which they encounter those items (Smith and Remington, 1996). Thus, a seemingly low Levins' niche breadth could be attributed to an animal whose real niche breadth was actually high. Unfortunately, I do not have the requisite information on prey availability to the murres to determine how a diet with the highest possible niche breadth would be composed. Even an estimate of the relative abundances of all possible chicks diet items would be insufficient for this purpose, because the murres' ability to perceive, catch and handle prey probably varies with prey type. Given that each of the items in the murres' chick diets is probably not equally available to their parents, my calculated niche breadths are probably underestimates and should be considered minima.

Although one can adhere only tenuously to conclusions about murre chick diet gleaned from niche breadth, diversity and overlap indices, the use of Monte Carlo randomization in this study is a step forward in the interpretation of such diet characteristics for seabirds. As Tokeshi (1986) has pointed out, ". . . it is now accepted that observed ecological patterns should be rigorously evaluated against randomized null models before deriving any inference from them." Despite this "acceptance," researchers rarely test their diet index scores against null models and so risk drawing specious conclusions from them. For example, authors of diet comparison papers often infer resource partitioning and even interspecific competition in part from reported high levels of diet overlap among the organisms they study, without testing to insure that those levels are higher than would occur randomly (Murie, 1995; Ebensperger and Botto-Mahan, 1997; Taber *et al.*, 1997) Although there seems to be no standard definition of high or low diet overlaps, researchers tend to assume that standardized index scores over 0.55 are high. However as the results of this study evince, given a limited range of diet items, overlap scores much larger than 0.55 would regularly occur randomly.

3.5.2 Chick diet overlap

I found no clear evidence of resource partitioning along any of the dimensions I measured. Nonetheless, I can not conclude with certainty that the murres occupied identical chick-food niches. This is because some of the data I collected are indicative of, but do not verify total resource use overlap. For instance, although chick diet overlap seemed high in both years, only in 1996 was such convergence higher than it would be by chance. Despite this, I have no reason to believe that the murres did not partition their chick diets in either year. This is because in both 1996 and 1997, their observed diet overlap was either well within or higher than the 95% confidence limits around the mean overlap from random diets. Thus, the murres' chick diet did not overlap less than predicted by the null model.

As with niche breadth estimates, conclusions about resource partitioning drawn from diet overlap estimates depend on the assumption that each item in the murre chicks' diets was equally available to their parents. If this assumption holds true, then the lack of adherence of an overlap value to the null model would indeed implicate resource partitioning. However, if shared rare items (such as gadids) in the chicks' diets were highly available to the parents, or if shared common items (such as shannies) were relatively unavailable to the parents, then lack of adherence to the null model could occur even in the absence of partitioning.

3.5.3 Chick rearing period

For 1996, the year in which diet overlap was significant, the only other resource partitioning possibility I examined was the timing of the chick-rearing period. In this, the two murre species overlapped entirely. But in 1997, the birds' chick food resource use appeared to converge along a greater range of parameters, including fish size and reproductive state, dive depth and possibly temporal foraging patterns.

3.5.4 Size, sex and reproductive state of fish delivered to chicks

The results of the comparison of the sizes and reproductive states of daubed shannies delivered to chicks in 1997 are unequivocal. The lengths and masses of these fish, the principal item in both murres' chick diets, did not vary significantly between species. Moreover, both species relied more heavily on gravid than non-gravid daubed shannies. Because daubed shannies comprised the greatest portion of the chick diets of both species, this indicates that Common and Thick-billed Murres did not divide their resource use by feeding their chicks fish of different sizes or reproductive states.

As at the Gannet Islands, at Hornoy in the Barents Sea, Common and Thick-billed Murres fed their chicks fish of the same size (Furness and Barrett, 1985; Barrett and

Furness, 1990; Barrett *et al.*, 1997). Yet these similarities are not universal. Also near Hornoy, Erikstad and Vader (1989) found that before the onset of egg-laying, Common and Thick-billed Murres feeding together on capelin schools took different sizes of fish. Using the lengths of fish in the stomachs of killed birds to guess the sex of the fish, they postulated that Thick-billed Murres might have taken more males than Common Murres took.

The disproportionate amount of non-gravid females among the capelin that Gannet Islands Common Murres fed their chicks is curious. Most of the capelin fed to murre chicks in the Barents Sea were gravid (Furness and Barrett, 1985; Barrett and Furness, 1990; Barrett *et al.*, 1997). The energy and protein content of gravid females is higher than those of other capelin (Montevecchi and Piatt, 1984), which *ceterus paribus* implies that the former would be preferred by foraging parents. If the murres' chick rearing period was late with respect to capelin spawning, this could explain the preponderance of spent and not-gravid females among the capelin that chicks ate. There is no longer a capelin fishery on the south Labrador coast, and I have no information on the timing of capelin spawning near the Gannet Islands.

3.5.5 Diurnal feeding pattern

Schoener (1974) has noted that more than other organisms, vertebrate predators tend to partition resource use by varying their time of activity. Because Common and Thick-billed Murres' timing of breeding was nearly identical during this study, if the murres engaged in temporal resource partitioning, they would have had to do so at a smaller scale. Whether or not they did this is uncertain; the diurnal feeding pattern data are ambiguous, offering evidence both for and against the hypothesis that Common and Thick-billed Murres forage for their chicks at different times of day. During one simultaneous all-day feeding watch, the birds exhibited similar feeding patterns, but during the other watch,

they did not. In speculation, it is less likely that the chick feeding routines of Common and Thick-billed Murres diverged than that they mirrored each other, because the number of Thick-billed Murre sites monitored was relatively low on the day during which their feeding did not peak significantly and did not follow the same pattern as the Common Murres'. And despite its' lack of *significant* peaks, the Thick-billeds' feeding pattern was similar to, albeit more subtle than the Common Murres' heterogeneous one.

Generally, early morning and afternoon feeding peaks characterized the feeding patterns of both species. Several constraints could account for this trend in feeding routines. Among these are the energetic demands of growing chicks and diurnal patterns in fish activity, either of which could account for early morning and afternoon feeding peaks. Another possibility was presented by McNamara *et al.* (1994), who showed that because of trade-offs between optimizing energy reserves, metabolic rates and responsiveness to predators, for small birds in winter, early morning and afternoon feeding peaks would be expected when food availability is high or when feeding is interrupted at unpredictable intervals. When food availability is low, the models of McNamara *et al.* predicted that feeding should remain constant throughout the day.

My data do not entirely corroborate either the chick demands thesis or the optimization model. In 1997, low food availability might explain the Common Murres' relatively uniform feeding routine of August 21. Feeding rates on this day were lower than during any other all-day feeding watch, and the proportion of capelin in the chicks' diets was little more than half of what is was during the other watches. In contrast, Common Murre feeding rates and diet composition in 1996 were similar during the all-day feeding watch without peaks (August 9) and those with peaks. For the Thick-billed Murres in 1997, feeding rates were higher during the watch without peaks (August 4), than during the one with peaks (August 10), and chick diet composition was virtually identical on both days. These patterns suggest that food availability does not solely, or predictably,

determine the chick feeding routine of Common and Thick-billed Murres. My data are insufficient to address McNamara *et al.*.'s related claim that feeding routines reflect the degree of stochasticity in foraging interruptions.

If changes in chick energy requirements cause changes in daily feeding routines, these changes would occur at the same time relative to the median hatch date each season. This was not the case with Common Murres. In 1996, the day without feeding peaks occurred one week after median hatch date, while in 1997 it occurred over three weeks after median hatch. An understanding of the predictability (to murres) of foraging success as well knowledge of the adults' self-feeding routines would be necessary to better explain the observed trends in the chick-feeding patterns of Common and Thick-billed Murres.

3.5.6 Dive depths

The dive depth data I collected were equivocal. They did indicate that Common and Thick-billed Murres exploited the same portion of the water column (diving to maximum depths between approximately 80 and 180 meters). And they did mesh with those reported for Thick-billed Murres at Coats Island (Croll *et al.*, 1992) and for Common Murres in Witless Bay (Piatt and Nettleship, 1985). Nevertheless, the Common Murre sample size (n=2) was too small from which to make reliable comparisons. Even if both species dove to the same mean maximum depths, as these data imply, they might have fed at different depths. Although the mean maximum dive depth of Thick-billed Murres breeding at Coats Island was 107m, the birds spent most of their dive time at 21-40 metres (Croll *et al.*, 1992). This indicates that murres' maximum depth is not necessarily a good proxy for time spent at depth. Similar foraging depth does not follow from similar diet composition; the daubed shannies that predominated murre chicks' diets occur at a wide range of depths (Coad *et al.*, 1995; Makushok, 1986; Scott and Scott, 1988). Thus, despite their chick diet

and maximum dive depth overlap, Common and Thick-billed Murres might not have foraged at the same depths.

If the Gannet Islands murres did not partition their chick diet resources, then their case would contradict Gause's Law. This law, which is predicated on the competition that Darwin (1859) envisaged, assumes that a single pool of resources is insufficient to support two species. The resource partitioning that Gause's Law predicts is often used to infer competition. Ironically, evidence of high levels of resource use overlap has also been called upon to verify the existence of interspecies competition. However, inferring competition from either high *or* low levels of resource use overlap is spurious (Schoener, 1974; Colwell and Futuyma, 1971; Pianka, 1981).

A more rigorous way to infer competition is by measuring the effects of one species on the population size or productivity of another (Pianka, 1981; Schoener, 1983). I do not have estimates of these parameters for either murre species breeding in the absence of the other at the Gannet Islands. But I do have estimates of these parameters for each species both before their chicks' diets exhibited high degrees of overlap and in 1996 and 1997, when they overlapped considerably. The chick diet overlap scores in 1982 and 1983 were 0.62 and 0.41 (calculated form data in Birkhead and Nettleship, 1987c) as compared to 0.98 and 0.77 in 1996 and 1997. Neither the breeding success of Common Murres nor that of Thick-billeds was lower in 1996 or 1997 than in 1981 (a year for which diet composition data are unavailable), 1982 or 1983 (Chapter 2; Birkhead and Nettleship, 1987b). Likewise, in 1996 and 1997, the colony attendance of both murres was the same as or higher than that recorded in 1981, 1982 and 1983 (Chapter 2). Hence, I detected no evidence of increased interspecific competition between the 1980s and 1990s.

I did not examine in depth the murres' "zones of foraging at sea," and so can not address Cody's (1973) proclamation that sympatric alcids segregate their resource use by

foraging at difference distances from their colony. Yet Bédard (1976) disproved Cody's suggestion when he used Cody's own data to show that members of both Atlantic and Pacific auk communities tend to forage at the same distances from their colonies. Bédard's counterargument has since been fortified by empirical studies. For example, based on crude estimates of foraging trip distance, Common and Thick-billed Murres' foraging ranges at Hornoy were found to be the same (Furness and Barrett, 1985).

Even if birds forage at the same distance from the colony, they can minimize their resource use overlap by foraging from different locations at the sea surface, at different depths, or on prey clumps of different densities. In Witless Bay, Newfoundland, Atlantic Puffins and Common Murres both fed their chicks capelin, but preyed upon aggregations of different densities and at different depths (Piatt, 1987; 1990). Because the birds' differences in foraging preferences increased with increasing prey availability, such differences were probably a proximate function of their different energy requirements (Piatt, 1990). It is possible that Gannet Islands murres segregated their foraging effort by exploiting different densities of fish, but this is unlikely. Although the behaviour of their principal chick food item is not well documented, given what is known about phyolgenetically and ecologically similar benthic fish, the daubed shanny probably does not aggregate.

Most of the studies that have lent credence to the competitive exclusion principle have been conducted in the tropics or in temperate regions. Of the 150 field studies demonstrating interspecific competition for resources reviewed by Schoener (1983), only three occurred in the Arctic, and none examined marine arctic systems. This could reflect a relative dearth of arctic marine ecological studies, or it could indicate an important difference between these and tropical or temperate systems. When they failed to detect strong evidence of competition between alcids breeding on Hornoy, in North Norway,

Furness and Barrett (1985) surmised that in the summer, high-latitude marine ecosystems might foster interspecies ecological similarity.

During the summer, Arctic marine productivity is higher than anywhere else on earth (Ocean Color from Space; Polar Productivity, 1998). The brevity of the season might make it difficult for sympatric species to stagger their breeding seasons. And the Arctic summer's explosive productivity might temper potential interspecies competition. Although the high productivity in high-latitude waters during the summer might lead to an abundance of resources, it does not precipitate a great diversity of those resources. Thus, while a tropical forest bird community and an Arctic seabird community might have the same amount of energy available to them, that energy might come in the form of 20 food types in the tropics, but only five in the Arctic. The Arctic's high summertime marine biomass and lack of diversity might facilitate high resource use overlap between ecologically similar species.

3.5.7 Conclusions

These data strongly suggest, but are inadequate to confirm that chick diet resource partitioning might have been negligible between Common and Thick-billed Murres at the Gannet Islands. Further investigations into time spent at depth and patterns of food delivery to chicks, as well as information about the locations from which the birds forage are needed to investigate this contention.

Table 3.1: Common and Thick-billed Murre chick diets, diet diversity, food-niche breadths and diet overlaps in 1996 and 1997.

prey item	percentage by number of chicks' diet 1996		percentage by number of chicks' diet 1997	
	Common Murre	Thick-billed Murre	Common Murre	Thick-billed Murre
capelin (*Mallotus villosus*)	11.8	1.8	44.7	6.3
blennies (family stricheaidae)	84.0	97.2	52.9	93.7
fish doctor (*Gymnelis viridis*)	1.4	0.9	—	—
gadids (family gadidae)	0.6	—	0.8	0.7
sandlance (*Ammodytes hexapterus*)	1.6	—	1.0	—
sculpin (*Myxocephalus sp.*)	0.6	—	0.3	—
squid (*Illex sp.*)	—	—	0.3	—
diversity (H')	0.550	0.135	0.816	0.269
niche breadth	0.065	0.181	0.024	0.006
niche overlap	0.982		0.769	

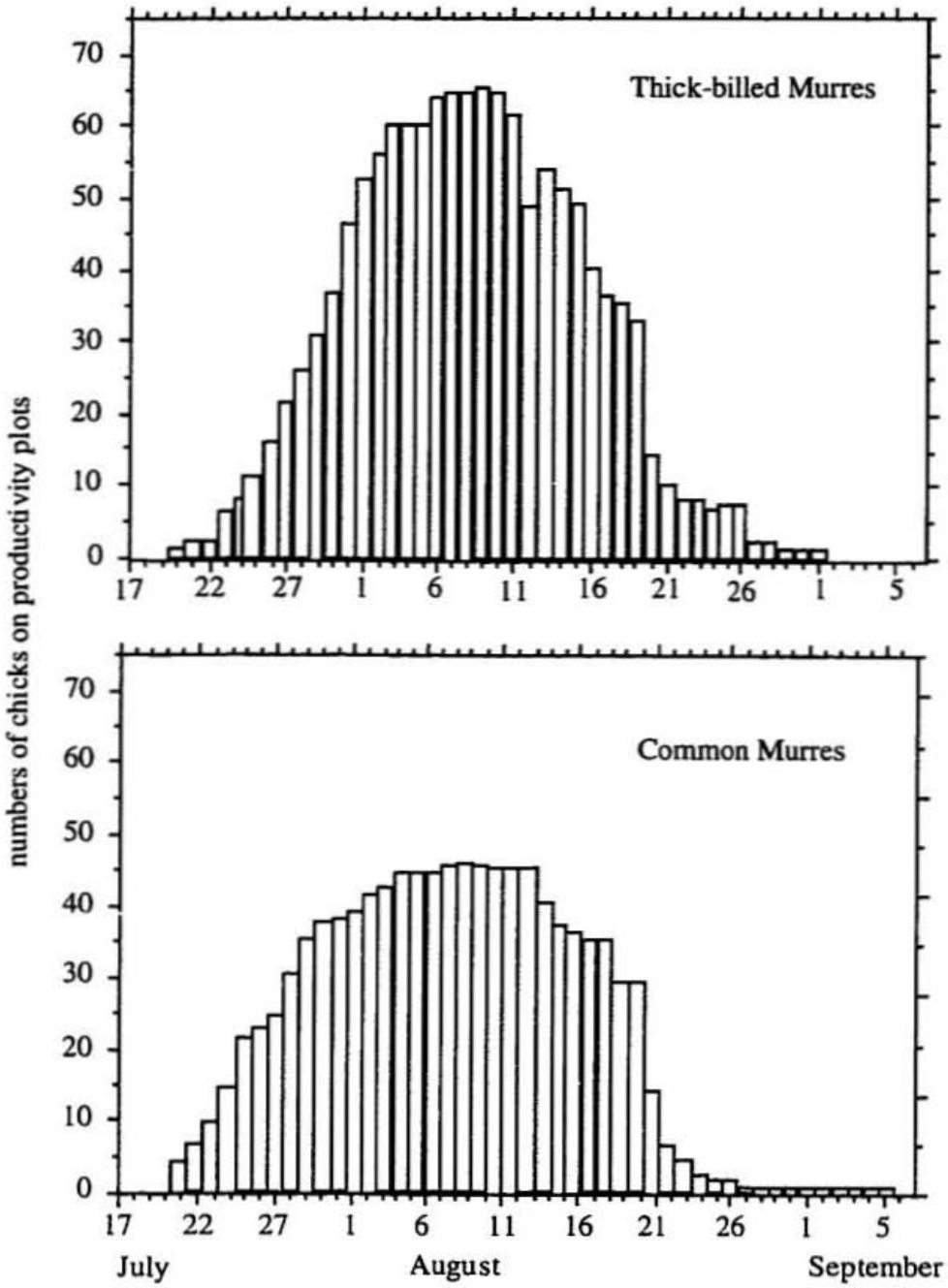

fig. 3.1: Numbers of Thick-billed and Common Murre chicks present on productivtiy plots during the chick rearing period in 1996

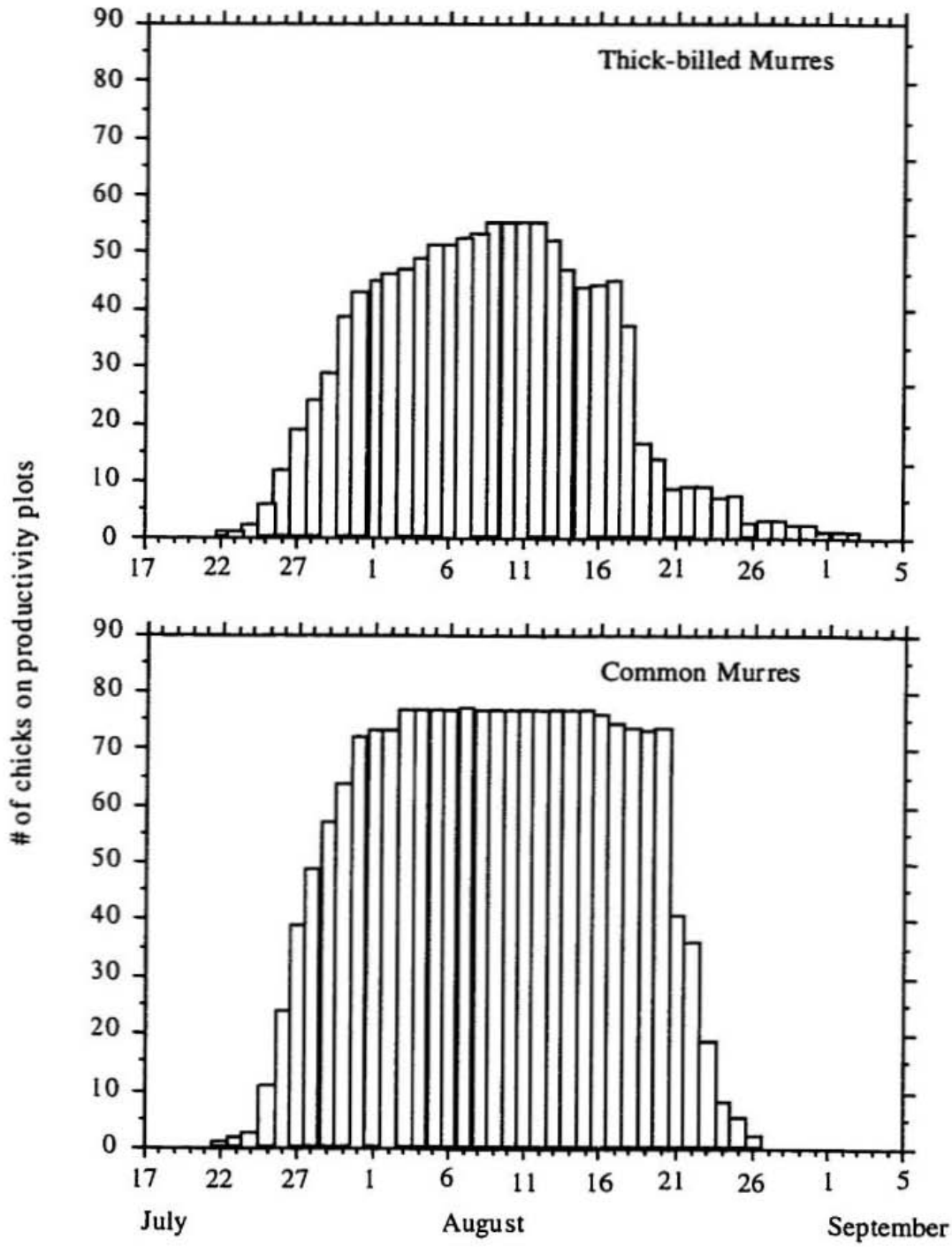

fig 3.2: Numbers of Common and Thick-billed Murre chicks present on pr ductivity plots during the chick rearing period in 1997

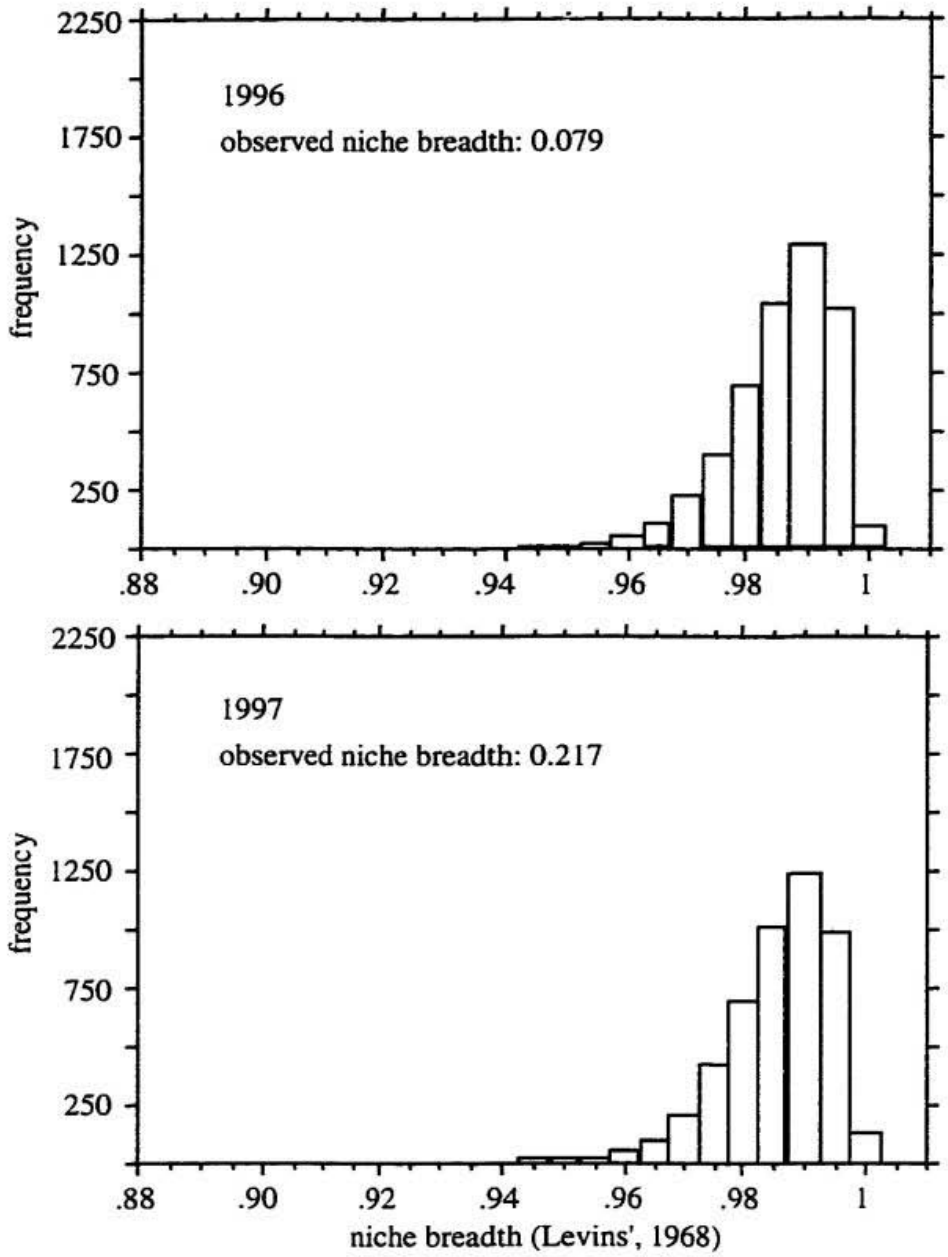

fig. 3.3: Freqeuncy distributions of 1996 and 1997 Common Murre chick diet niche breadths derived from 5000 randomized diet compositions

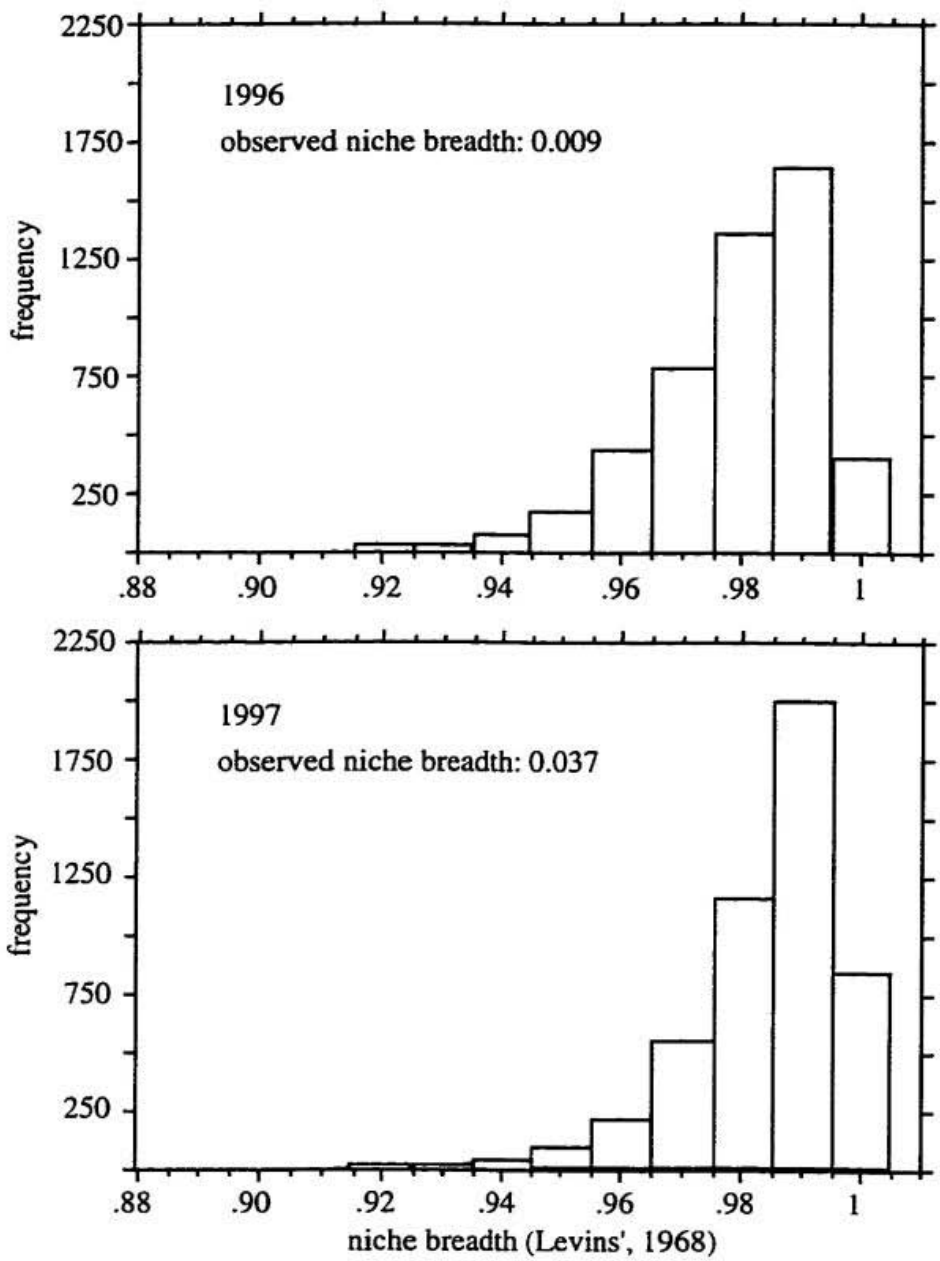

fig 3.4: Freqeuncy distributions of 1996 and 1997 Thick-billed Murre chick diet niche breadths derived from 5000 randomized diets compositions

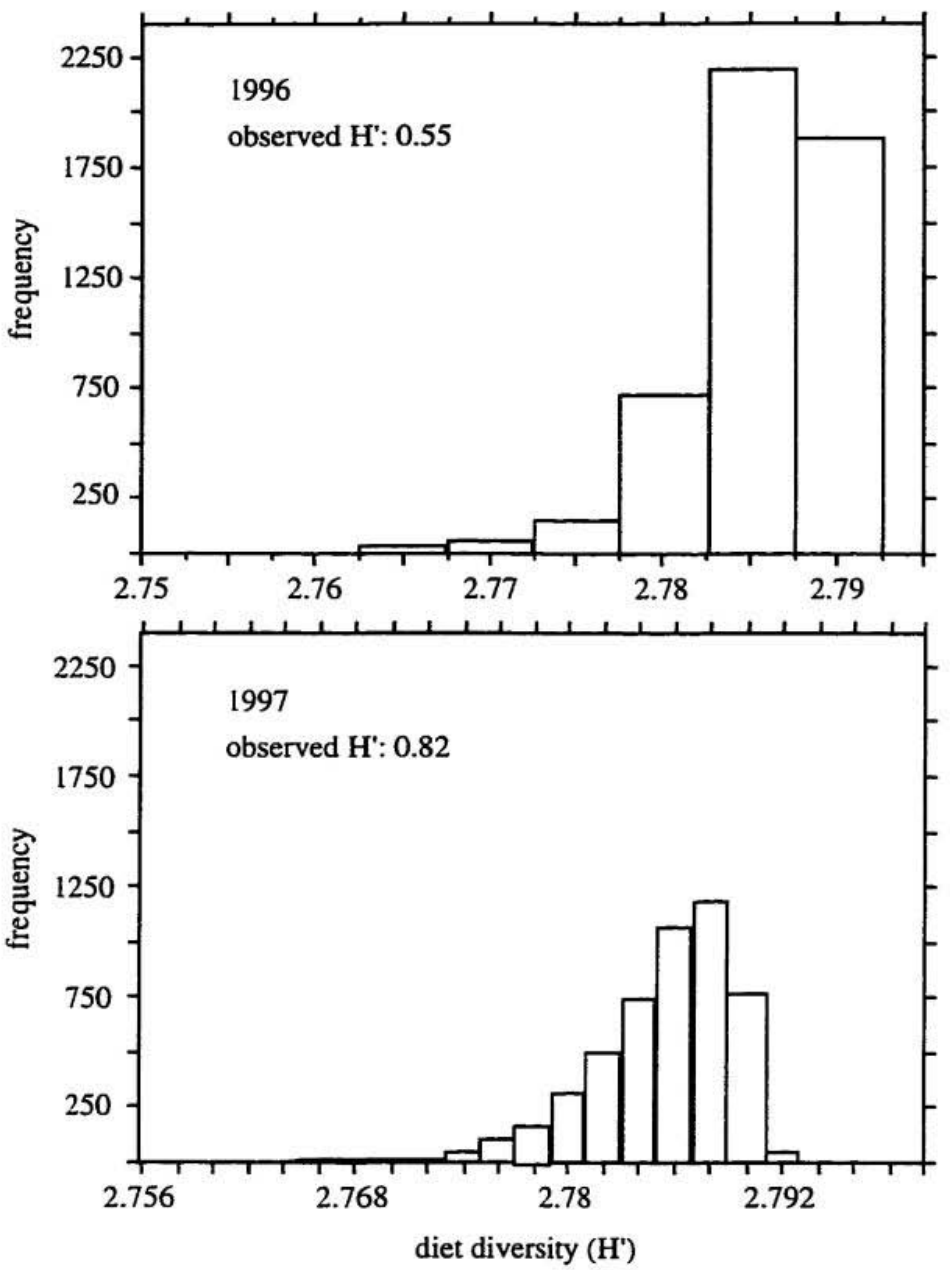

fig 3.5: Freqeuncy distributions of 1996 and 1997 Common Murre chick diet diversities derived from 5000 randomized diet compositions.

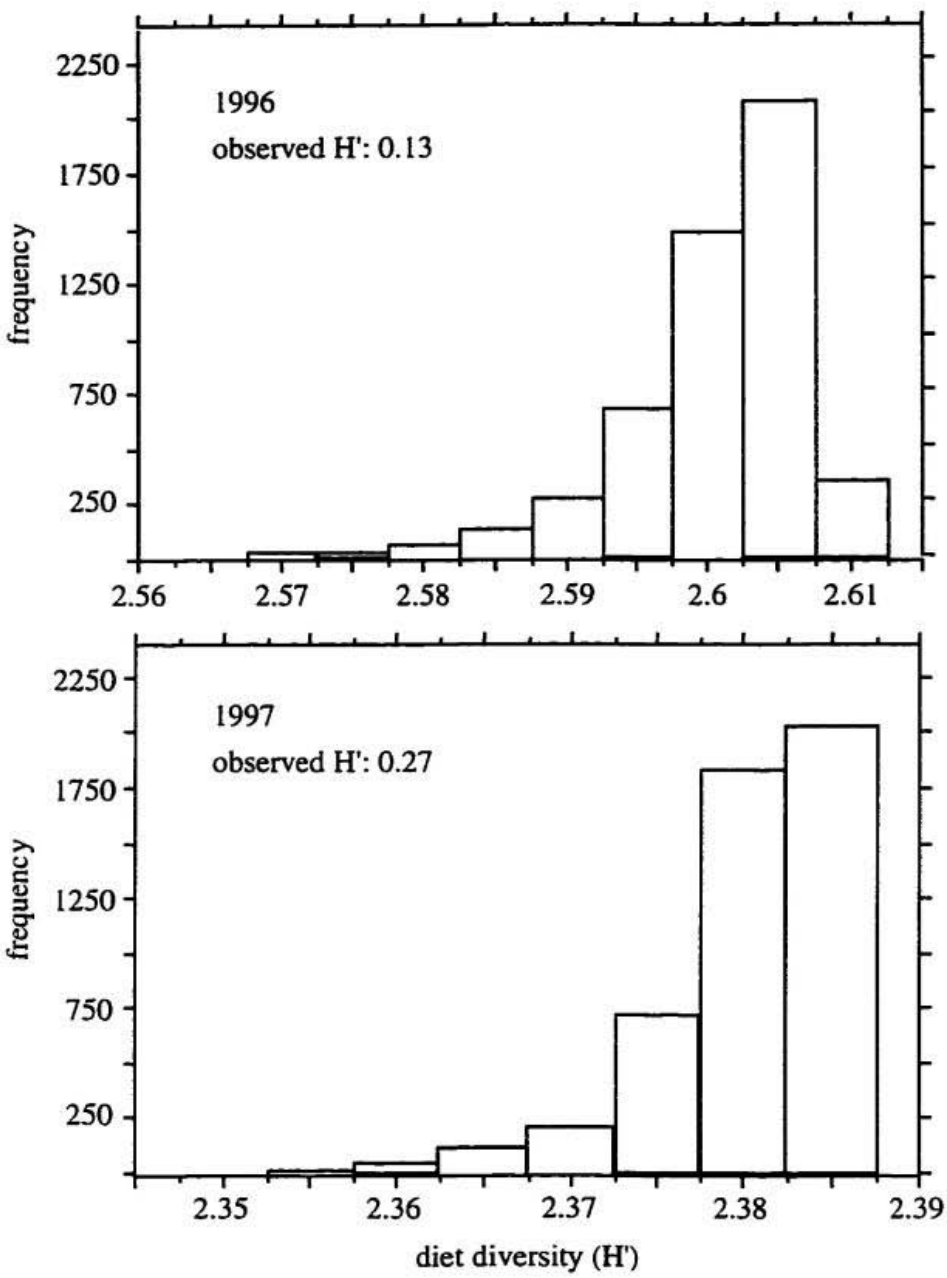

fig 3.6: Freqeuncy distributions of 1996 and 1997 Thick-billed Murre chick diet diversities derived from 5000 randomized diet compositions

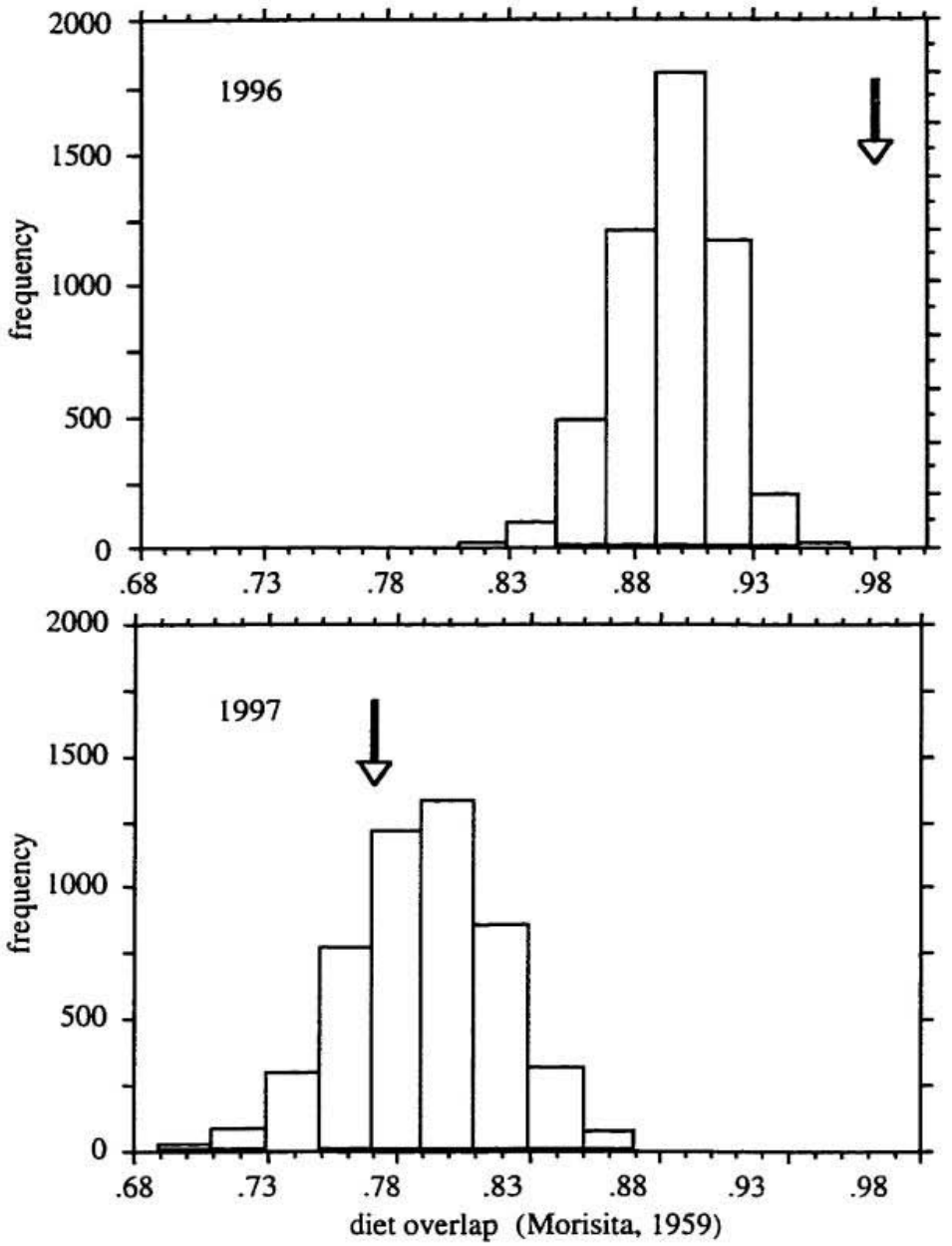

fig. 3.7: frequency distribution of Common and Thick-billed Murre chick diet overlaps calculated from randomly generated diets, given the number of fish deliveries and species of fish fed to chicks of each species in 1996 and 1997. Arrows indicate observed overlaps.

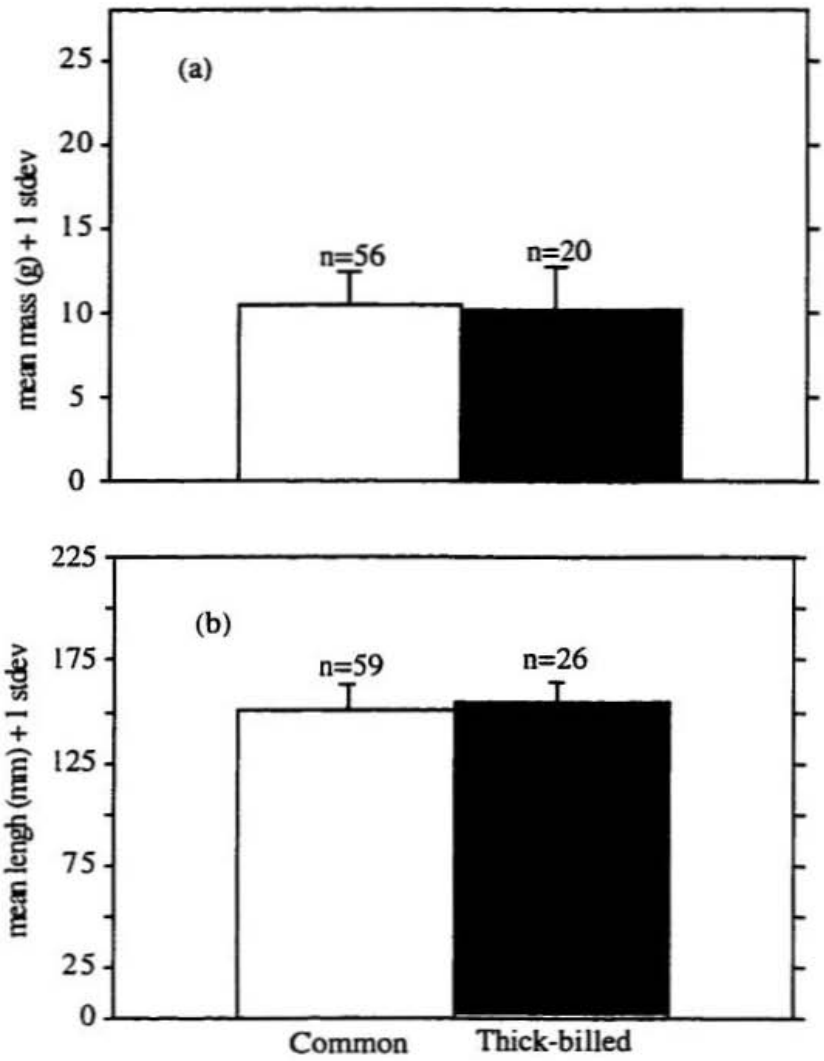

fig 3.8: Sizes of daubed shannies delivered to Common and Thick-billed Murre chicks in 1997: (a) mean mass; (b) mean total length

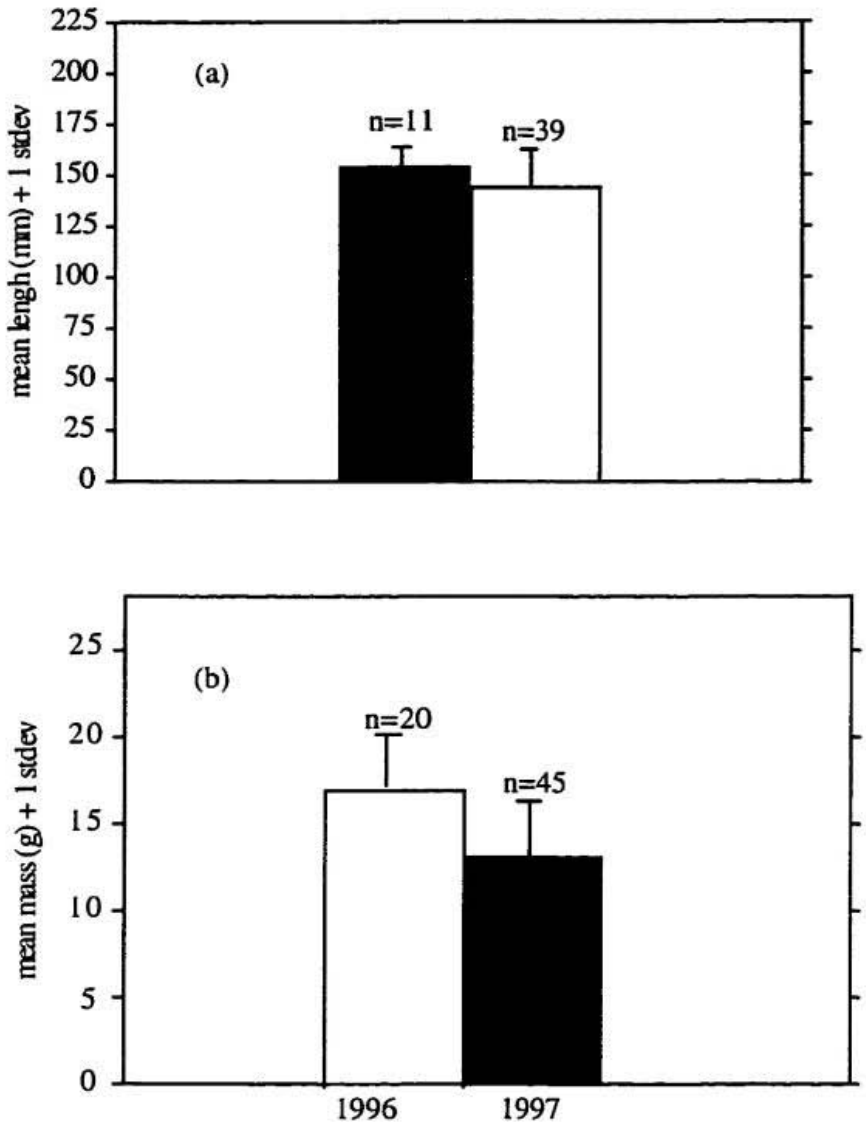

fig 3.9: sizes of capelin delivered to Common Murre chicks in 1996 and 1997: (a) mean fork lenths; (b) mean masses

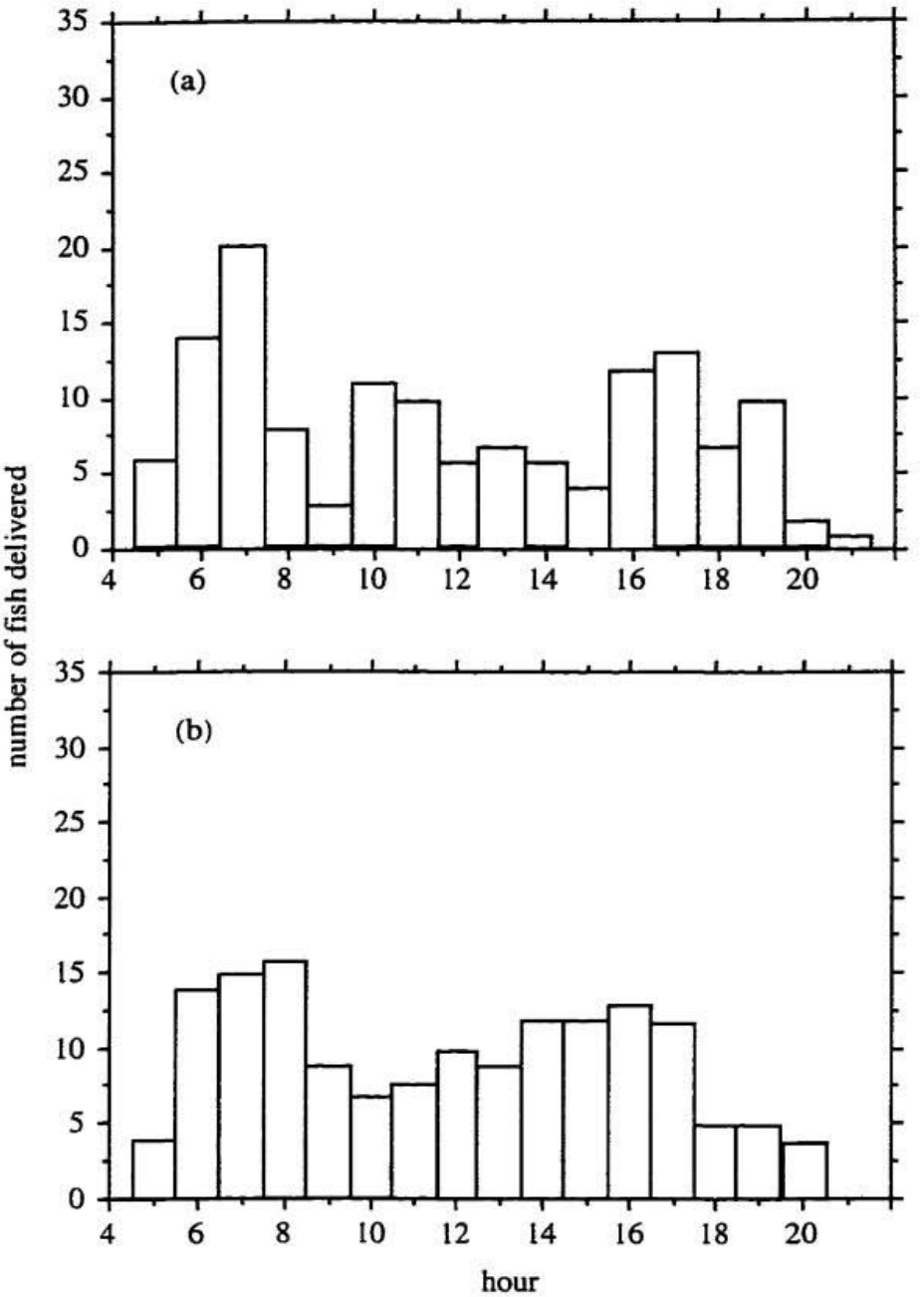

fig 3.10: Numbers of fish delivered to Common Murre chicks on feeding watch plots each hour during 0400 h - 2130 h feeding watches on August 4 (a), and August 9 (b) 1996. Thirty-eight sites on the plot had chicks on August 4, and 44 sites had chicks on August 9.

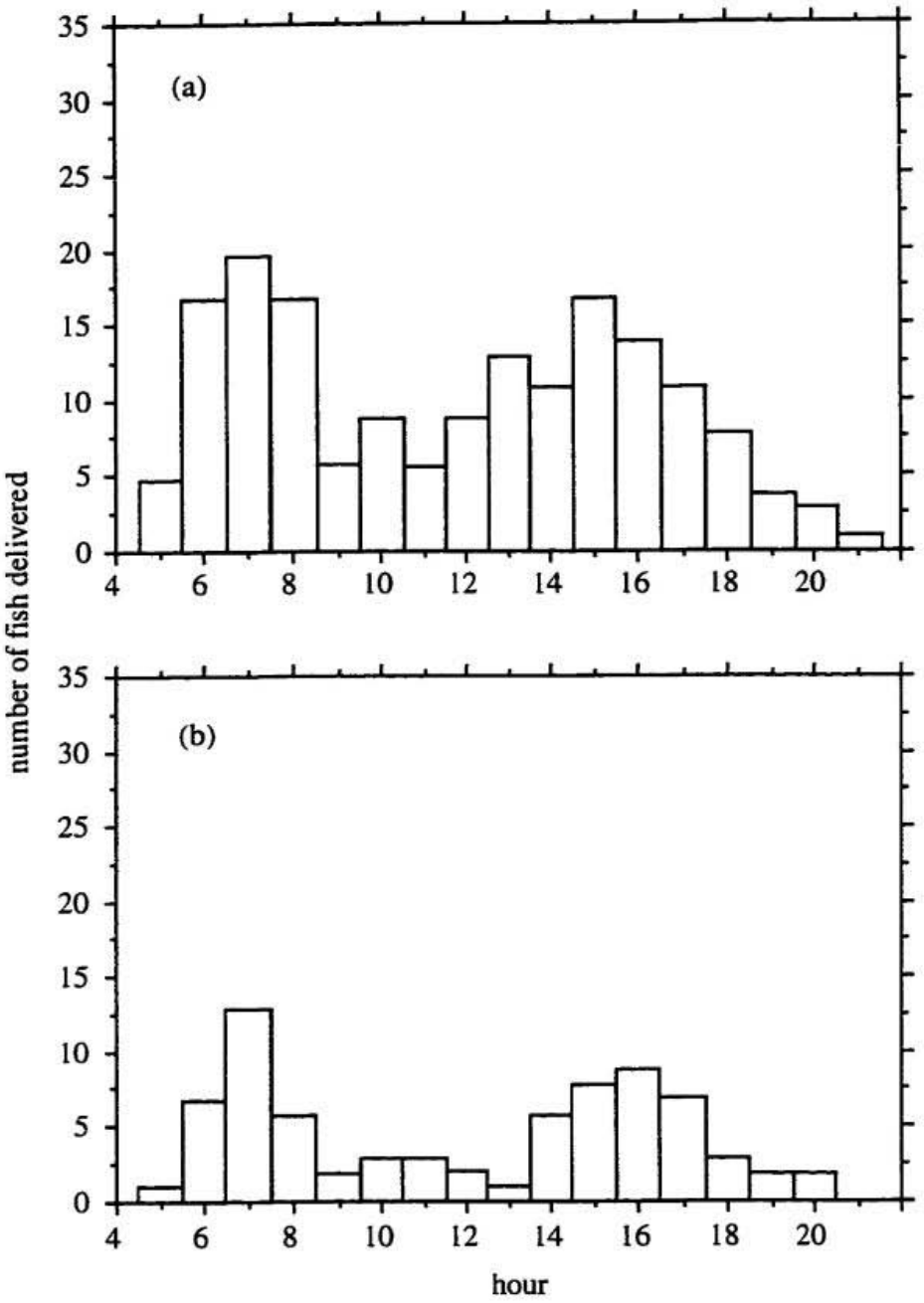

fig 3.11: Numbers of fish delivered to Common Murre chicks on feeding watch plots each hour during 0400h - 2130 h feeding watches on August 16 (a), and August 21 (b) 1996. Forty-three sites on the plot had chicks on August 16, and 28 sites had chicks on August 21.

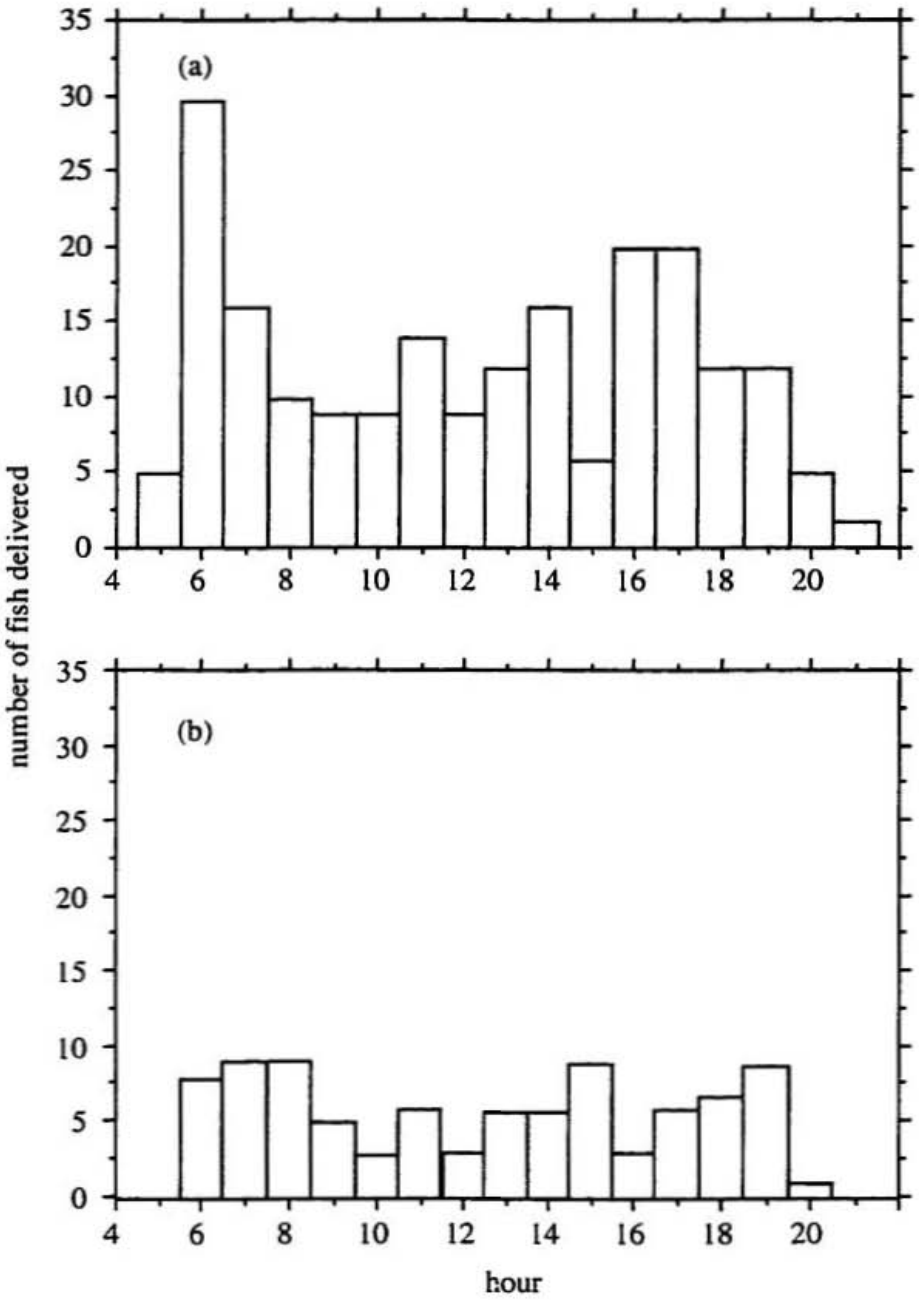

fig 3.12: Numbers of fish delivered to Common Murre chicks on feeding watch plots each hour during 0400h - 2130 h feeding watches on August 9 (a), and August 21 (b) 1997. Forty-nine sites on the plot had chicks on August 9, and 29 sites had chicks on August 21.

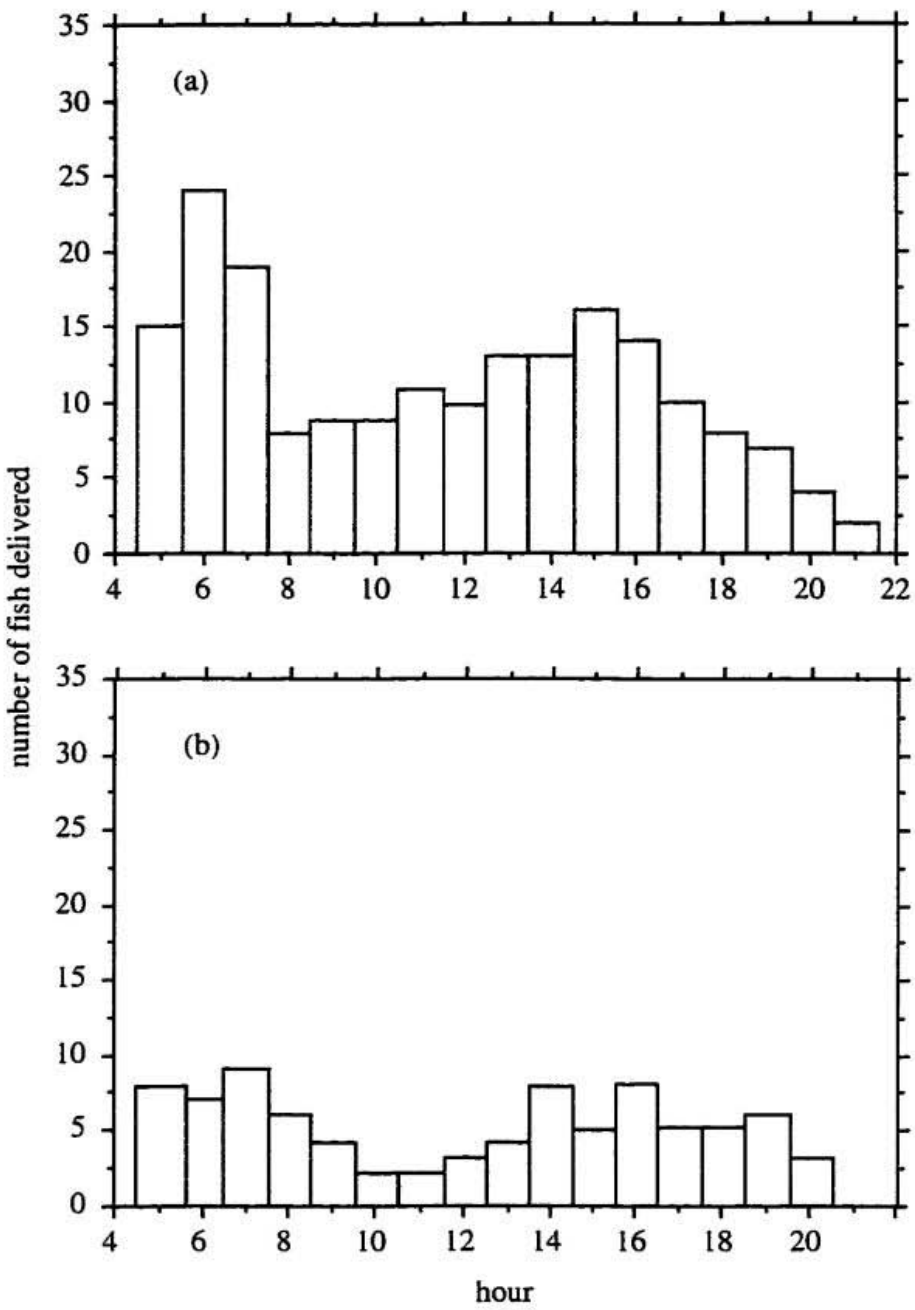

fig 3.13: Numbers of fish delivered to forty-five Common (a) and twenty-four Thick-billed Murre (b) chicks on feeding watch plots each hour during a 0400h - 2130h feeding watches on August 5, 1997.

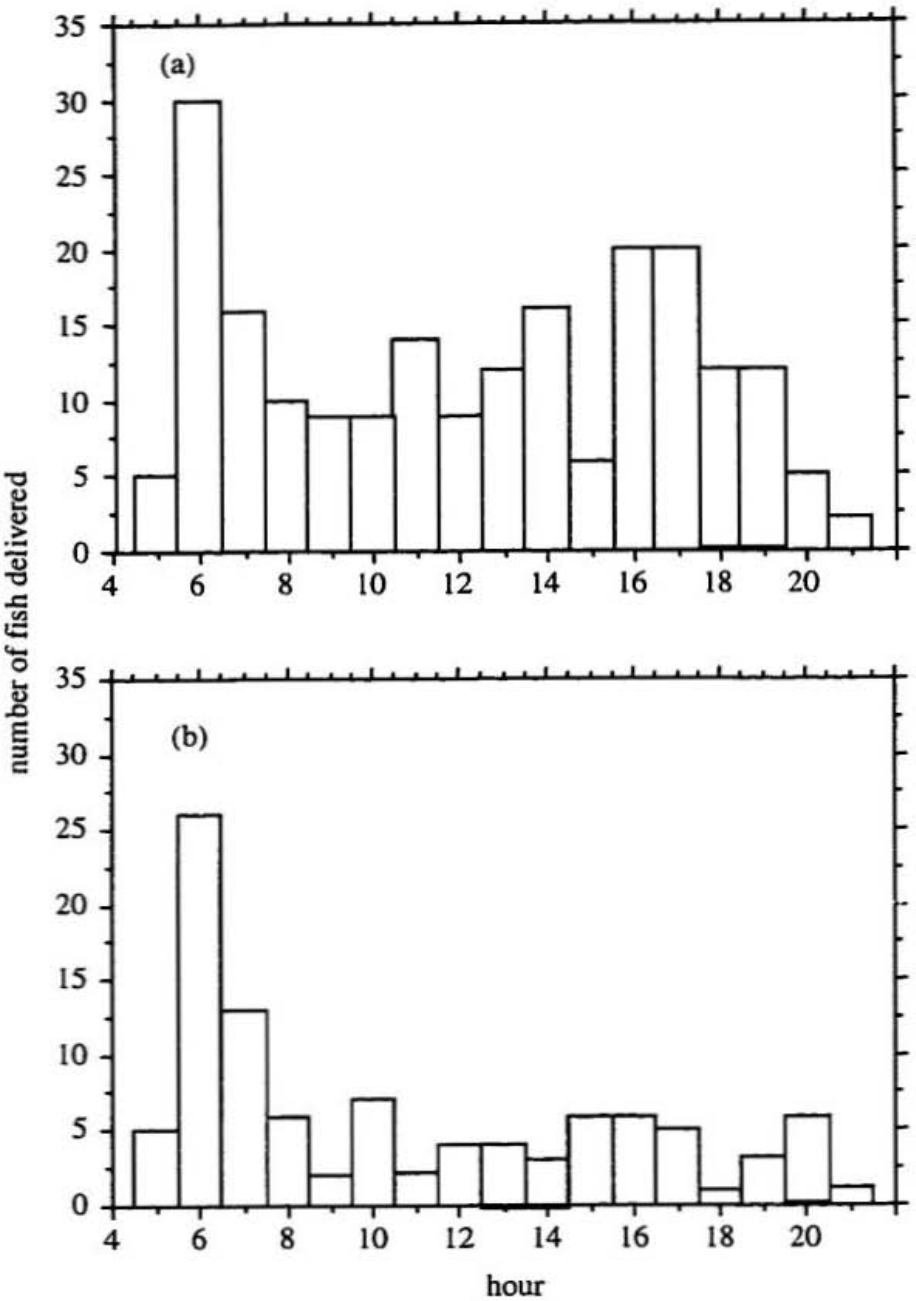

fig 3.14: Numbers of fish delivered to fifty Common (a) and twenty-eight Thick-billed Murre (b) chicks on feeding watch plots each hour during a 0400 h - 2130 h feeding watches on August 19, 1997.

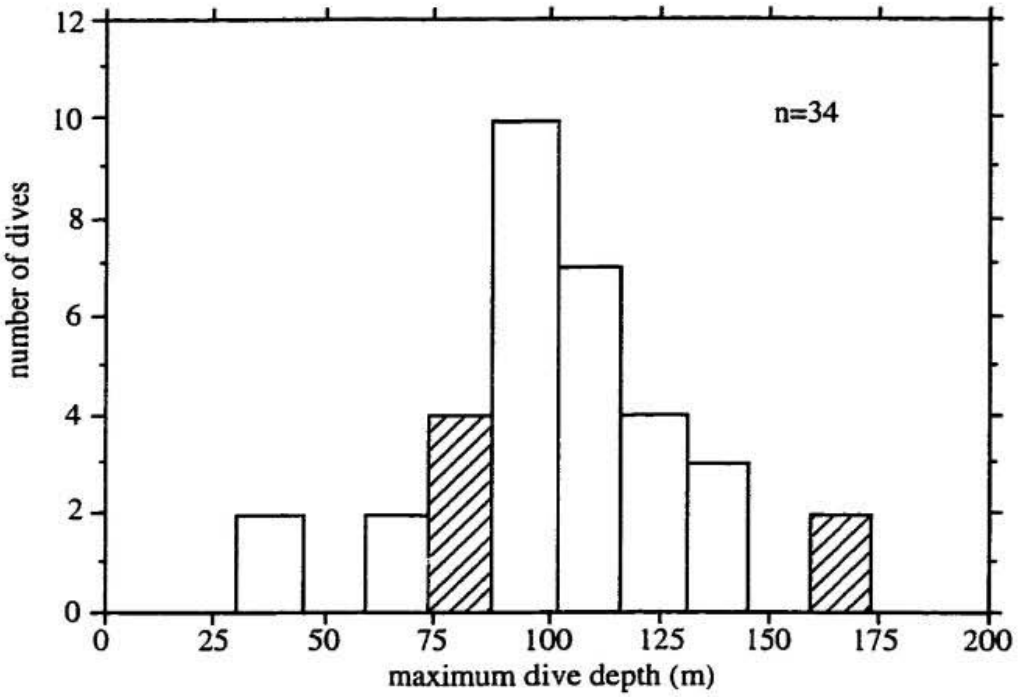

fig 3.15: Maximum dive depths of breeding Thick-billed Murres in 1996 and 1997. Hatched bars indicate intervals that include maximum depths to which Common Murres (n=2) dove. Common Murre dives are not included in number of dives per interval.

CHAPTER 4

GENERAL DISCUSSION

The two lines of harmony investigated in this thesis are probably variations on the same theme. In other words, both the Gannet Island murres' apparent lack of negative response to capelin scarcity, as well as their apparent lack of chick diet resource partitioning might be related responses to a single condition. An abundance of suitable fish other than capelin for the subsistence of their chicks could explain both the murres' resource use overlap and their robustness to changes in capelin abundance. A better understanding of the daubed shanny's behaviour and ecology could strengthen the conceptual link between the murres' resource use and putative lack of resource partitioning. This is largely because patterns of resource use and of resource partitioning both seem to respond to resource availability.

The ecological literature, including that pertaining to seabirds as bioindicators, swells with examples of how resource use fluctuates with resource availability (Hunt *et al.*, 1996; Montevecchi *et al.*, 1988; Montevecchi and Myers, 1995; Crawford and Dyer, 1995, Cullen *et al.*, 1992; Hobday, 1992). And despite the popular assumption among nineteenth and twentieth century biologists that resources are necessarily limiting and universally partitioned between species, it seems as though the extent of interspecies partitioning varies with resource abundance. For instance, in the Potholes region in north western U.S.A., syntopic Red-Winged, Yellow-headed and Brewer's Blackbirds foraged together on the same aquatic insects during the middle of the day - when the bugs were abundant - and segregated their foraging effort when they were scarce (Orians, 1972).

Orians' blackbird study does not provide the only precedent for resource-sharing among birds when resources are plentiful. Cody (1974) wrote: "There are instances in bird

communities where resources are apparently nonlimiting and are used by many species in similar ways." These include the incidence of cooperative feeding among alcids and larids. On the west coast of North America, Rhinoceros Auklets (*Cerorhinca monacerata*) and Marbled Murrelets (*Brachyramphus marmoratus*) together dive so as to coalesce sandlance shoals and herd them towards the surface. Then they plunge below the dense aggregation of fish to feed on it (Grover and Olla, 1983; Hoffman *et al.*, 1981). Along with gulls and terns, Common Murres, Tufted and Horned Puffins take advantage of these forced congregations of fish. Penguins, too, often feed in mixed-species groups (Wilson, 1995). Perhaps within these feeding frenzies birds of different species take different sizes or sexes of fish, as has been shown for Common and Thick-billed Murres feeding together on capelin in the Barents Sea (Erikstad *et al.*, 1989).

The above examples illustrate that although many ecological situations seem to follow Gause's law, adherence to the law should not be considered inevitable. We might not find evidence of resource partitioning because we aren't looking hard enough, or at the right times in the right places. *Or* we might not find it simply because it does not happen; Gause's Law might not be universally applicable. Both logical and empirical arguments support this.

Gause's Law follows from Darwin's principle of natural selection, and Darwin's principle rests on Malthus' assertion, which is flawed. Darwin's (1859) position that "there *must in every case* be a struggle for existence" (italics mine) was leant credence by the popularity of Malthus' (1803) untested claim that a discrepancy between the geometric rate of increase of user populations and the arithmetic rate of increase of resource populations is inevitable. The fact that resources themselves are often user populations, and thus according to Malthus should at once increase geometrically *and* arithmetically weakens his doctrine (Fisher, 1988).

If the claim that populations necessarily increase at a greater rate than their subsistence is unfounded, then the concomitant ideas of "existence as an incessant struggle" and of the ubiquity of competition for resources are deflated. This is not to say that resources are never scarce, or that competition is not an important natural selective force. Rather, it is simply to say that in some cases the competitive exclusion principle might fail to explain ecological relationships between sympatric congeners. These cases would include situations in which resources are sufficiently abundant to support more than one population. Cody (1974) recognized the impossibility of competition for abundant resources when he wrote: "no displacement patterns can evolve on superabundant resources, which can be simultaneously and similarly used by several species."

These objections are not fatal to the competitive exclusion principle, but they do warrant some caveats. The principle can be amended to state that *when* resources are scarce, sympatric species will not share them. This increases the law's explanatory power, rendering it consistent with the empirical evidence that once balked it. The superabundance of resources that facilitated the resource sharing suggested by Cody (1974) and documented by Orians (1972) for blackbirds and by other researchers for seabirds were ephemeral; the bird predators sounded the same ecological melody for only one measure at a time. Yet extreme transience does not necessarily characterize abundance, so different predator populations could play in tandem for entire movements of an ecological score. Such meso-term resource abundance might be more likely to occur in oceanographically arctic ecosystems than in other ecosystems because of the seasonally high abundance and low diversity that characterize the former. Thus, consistently high abundances of fish near the Gannet Islands in the summer could explain the possibility that throughout their chick-rearing periods, Common and Thick-billed Murres did not partition their chick diet resources.

This hypothesis would make sense if daubed shannies were both highly available to and sufficiently energetically rich for the murres. Not much independent evidence exists to support or reject the former possibility, but the results of proximate analysis suggest that at the Gannet Islands, the energy density and fat content of daubed shannies are equally as high those capelin (Lawson *et al.* 1998; Magalhaes, 1998, and see Chapter 2).

The scant data on the daubed shanny's distribution begin to demarcate the fish's geographic range (Scripps Institute of Oceanography Oceanographic Collections 1997; NMNH Fish Collection, 1998; UWFC Search Interface, 1998, and see Chapter 2), but its abundance within this range is poorly understood (East Coast of North America Strategic Assessment Project, 1998, and see Chapter 2). Information on the daubed shanny's behaviour is even more scant than data on its abundance and distribution. It is also spurious, contradicting the information that can be garnered from birds. For instance, most sources report that daubed shannies spawn in the winter (Makushok, 1986; Scott and Scott, 1988; Coad *et al..*, 1995) but the majority of the fish that murres delivered to their chicks in the summer were gravid.

The paucity of basic life history and distribution data for the daubed shanny is unfortunate, given that the fish figures prominently in the marine ecology of the Labrador coast (JWEL, 1997). This information gap might result from an understandably strong bias toward studying economically interesting species at the expense of non commercial, but ecologically interesting ones. The narrow research focus on commercially important species has impoverished our understanding of north west Atlantic marine ecology.

Are the ecological melodies of capelin and Common or Thick-billed Murres tightly enough entwined that by learning one we can divine the other? Breeding parameters Thick-billed Murres at the Gannet Islands seem sufficiently independent of capelin abundance that the former probably do not make good indicators the latter. Capelin do not appear to

be the Thick-billeds' preferred chick diet fish. They drop out of the chicks' diets when their abundance seems low, but not negligible. Likewise, one could expect a threshold of capelin in Thick -billed Murres' chick diets to be reached at only moderate levels of capelin abundance.

The results of this study indicate that the proportion of capelin in Common Murre chick diet might reflect the abundance of capelin in the southern Labrador Sea. It is not clear at which spatial or temporal scales this relationship holds. It is also not clear whether the percentage of Common Murre chicks' diets accounted for by capelin is linearly correlated to capelin abundance, and if it is, whether it affords predictions of capelin abundance on a nominal, ordinal or interval scale. Simple relationships between their chicks' diets and fish availability might be confounded by Common Murres' apparently high degree of flexibility in fishing behaviour. More than two years of diet and acoustic data are necessary to determine the precision with which Common Murre chick diet might indicate capelin abundance.

Looking to murre chick diet as a harbinger of capelin abundance should be done not without hope, but with caution and conservatism. In most cases in which seabird parameters have been shown to correlate with measures of prey abundance, they do so only for limited ranges of those abundances. At the scale of shoals of fish, for instance, there seem to be density thresholds below and above which auks are not sensitive to changes (Piatt, 1987, 1990; Hunt *et al.*, 1992). And at the scale of fish populations, Cairns (1992) hypothesized that the relationship between seabird parameters and prey abundance are sigmoidal, such that at very low and very high levels of the latter, the former do not change. Along these lines, Pat Monaghan (1996) has written: "It must be borne in mind that seabirds can only indicate variations in prey abundance at the lower end of the spectrum; above a certain threshold density, changes in prey abundance will not be

reflected in the behaviour of the birds since factors other than food supply will set the ceiling on their reproductive and foraging performance."

Landres *et al.*. (1988) warned against using any vertebrate population as an ecological indicator of another. They argued that populations that share habitats do not necessarily respond similarly to changes in habitat structure or quality, and therefore, trends of one species in a guild might not reflect those of another in sympatry. The position that one guild member does not *a priori* make a good indicator of another is valid, but does not necessarily apply to predator-prey relationships, which are more direct and causal than those between guild members. Still, the cautions of Landres *et al.* against assuming that two populations will respond similarly to environmental change, and against using one population as the only indicator of another are invaluable to a program that attempts to use seabirds as indicators of the abundance of their prey.

Whether and to what extent murre chick diet reflects fish abundance hinges on the foraging strategy of adult murres. The degree to which the birds behave selectively when catching fish in part determines which species (or group of species) their chicks' diets might indicate, and at which levels of abundance or availability. For instance, if murres are complete dietary generalists, they will take fish in the exact proportions in which they encounter them, and chick diet will then represent the relative abundances of fish within the birds' foraging range, given their perceptual abilities. However, it is more likely that murres spend more time foraging at some depths than at others, that they are better at catching some kinds of fish than others, and that they "prefer" to feed their chicks fish of a particular size and nutritional value. Understanding the birds' perceptual and locomotor abilities, as well as their effective prey choice criteria, is required to understand the degree to which their chick diets will fluctuate with prey abundance.

An understanding of the resource use patterns of breeding murres might also reveal the sets of conditions under which Common and Thick-billed Murres partition or share

resources. However preliminary, the results of this study intimate that conditions probably do exist under which resource partitioning is negligible. Despite the trend toward describing ecological differences, further inquires into ecological overlap would be meaningful:

> "Because of the well-established tradition of seeking differences among species, the literature is skewed toward documentations of patterns of ecological separation. Similarities, which are often more impressive, are frequently ignored or are considered bothersome details that obscure the features of critical interest. Our main concern in studying local assemblages *should* be with how the species use resources, and in this context similarity may be just as interesting as difference."
>
> - Wiens, 1989

Equally meaningful would be a description of the environmental conditions that support ecological overlap. A superabundance of daubed shannies in the vicinity of the Gannet Islands could account for the possibly high degree of chick diet resource use overlap between Common and Thick-billed Murres, as well as account for their reproductive imperviousness to a decline in capelin abundance. It seems as though in the symphony of the Labrador Sea, the importance of the daubed shanny is reaching a crescendo. In order to understand the ecology of Common and Thick-billed Murres and their responses to fluctuations in the abundance of their prey, it is imperative that we learn more about this enigmatic fish.

REFERENCES

Adams, D. C. and C. D. Anthony. 1996. Using randomization techniques to analyze behavioural data. Anim. Behav. 51: 733-738.

Ainley, D.G., W.J. Sydeman, and J. Norton. 1995. Upper trophic level predators indicate interannual negative and positive anomalies in the California Current food web. Marine Ecol. Prog. Ser. 118(1-3): 69-79.

Ainley, D. G., L. B. Spear, S.G. Allen and C. A. Ribic 1996. Temporal and spatial patterns in the diet of the Common Murre in California waters. Condor 98: 691-704.

Anderson, D. W. and F. Gress. 1984. Brown Pelicans and the anchovy fishery off southern California. *In* D. N. Nettleship, G. A. Sanger and P. F. Springer, Eds. Marine Birds: their feeding ecology and commercial fisheries relationships. Ottawa, Canadian Wildlife Service.

Barrett, R. T. and R. W. Furness. 1990. The prey and diving depths of seabirds on Hornoy, North Norway after a decrease in the Barents Sea capelin stocks. Ornis Scand. 21: 179-186.

Barrett, R. T. 1996. Prey harvest, chick growth, and production of three seabird species on Bleiksoy, North Norway, during years of variable food availability. *In* W. A. Montevecchi, Ed. Studies of High Latitude Seabirds 4. Trophic relationships and energetics of endotherms in cold ocean systems. Ottawa, Canadian Wildlife Service. Occasional Paper 91: 20-26.

Barrett, R. T. and Y. T. Krasnov. 1996. Recent responses to changes in stocks of prey species by seabirds breeding in the Southern Barents Sea. ICES J. Mar. Sci. 53: 713-722.

Barrett, R. T., M. Asheim and V. Bakken. 1997. Ecological relationships between two sympatric congeneric species, Common and Thick-billed Murres, *Uria aalge* and *Uria lomvia* breeding in the Barents Sea. Can. J. Zool. 75: 618-631.

Benvenuti, S., F. Bonadonna, L. Dall'Antonia and G. Gudmundsson. 1988. Foraging flights of breeding Thick-billed Murres *Uria lomvia* as revealed by bird-borne direction recorders. Auk 115(1): 57-66.

Bédard, J. 1976. Coexistence, coevolution and convergent evolution in seabird communities: a comment. Ecology 57(1): 177-184.

Birkhead, T.R. 1976. Breeding biology and survival of Guillemots *Uria aalge*. D. Phil thesis. University of Oxford, Oxford.

Birkhead, T. R. 1985. Coloniality and social behaviour in the Atlanic alcidae. *In* D. N. Nettleship and T. R. Birkhead, Eds. The Atlantic Alcidae. London, Academic Press.

Birkhead, T.R. and D.N Nettleship 1981. Reproductive biology of Thick-billed Murres *Uria lomvia*: an intercolony comparison. Auk 98: 258-269.

Birkhead, T. R. and D.N. Nettleship. 1982. Studies of alcids breeding at the Gannet Clusters, Labrador, 1981. Dartmouth, NS, Canadian Wildlife Service.

Birkhead, T. R. and D. N. Nettleship. 1985. Ecological relationships between alcids breeding at the Gannet Clusters, Labrador . Dartmouth, N.S., Canadian Wildlife Service.

Birkhead, T. R. and D. N. Nettleship. 1987a. Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador I. Morphometrics and timing of breeding. Can. J. Zool. 65: 621-629.

Birkhead, T. R. and D. N. Nettleship. 1987b. Ecological relationships between common Murres, *Uria aalge* , and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands,

Labrador II. Breeding success and site characteristics. Can. J. Zool. 65: 1630-1637.

Birkhead, T. R. and D. N. Nettleship. 1987c. Ecological relationships between Common Murres, *Uria aalge*, and Thick-billed Murres, *Uria lomvia*, at the Gannet Islands, Labrador III. Feeding ecology of the young. Can. J. Zool. 65: 1638-1649.

Birkhead, T. R., E. Greene, J.D. Biggins and D.N. Nettleship. 1985. Breeding site characteristics and breeding success in Thick-billed Murres. Can. J. Zool. 63: 1880-1884.

Bradstreet, M. S. W. and R. G. B. Brown. 1985. Feeding ecology of the Atlantic alcidae. *In* D. N. Nettleship and T. R. Birkhead, Eds. The Atlantic Alcidae. London, Academic Press.

Burger, A. E. and R. P. Wilson. 1988. Capillary-tube depth gauges for diving animals: an assessment of their accuracy and applicability. J. Field Ornithol. 59(4): 345-354.

Burger, A. E. and J. F. Piatt. 1990. Flexible time budgets in breeding Common Murres: buffers against variable prey abundance. Stud. Avian Biol. 14: 71-83.

Cairns, D. K., K. A. Bredin and W.A. Montevecchi. 1987. Activity budgets and foraging ranges of breeding Common Murres. Auk 104: 218-224.

Cairns, D. K. 1987. Seabirds as indicators of marine food supplies. Biol. Oceanogr. 5: 261-271.

Cairns, D., K. 1992. Bridging the gap between ornithology and fisheries science: use of seabird data in stock assessment models. Condor 94: 811-824.

Coad, B. W., H. Waczuk and I. Labignan. 1995. Encyclopedia of Canadian Fishes. Singapore, Canadian Museum of Nature.

Cody, M. L. 1968. On the methods of resource division in grassland bird communities. Am. Nat. 102(924): 107-147.

Cody, M.L. 1973. Coexistence, coevolution and convergent evolution in seabird communities. Ecol. 54(1): 31-44.

Cody, M.L. 1974. Competition and the structure of bird communities. Princeton, Princeton U. Press.

Colwell, R. K. and D. J. Futuyma. 1971. On the measurement of niche breadth and niche overlap. Ecology 52(4): 567-576.

Crawford, R. J. M. and B. M. Dyer. 1995. Responses by four seabird species to a fluctuating availability of Cape Anchovy Engraulis capensis off South Africa. Ibis 137: 329-339.

Croll, D.A., A.J. Gaston and D.G. Noble. 1991. Adaptive loss of mass in Thick-billed Murres. Condor 93: 496-502.

Croll, D. A., A. J. Gaston, A.E. Burger and D. Konnoff. 1992. Foraging behavior and the physiological adaptation for diving in Thick-billed Murres. Ecology 73: 344-356.

Cullen, J. M., T. L. Montague and C.Hull. 1992. Food of Little Penguins *Eudyptula minor* in Victoria: comparison of three localities between 1985 and 1988. Emu 19: 318-341.

Darwin, C. 1859. On the Origin of Species by Means of Natural Selection. London, Murray.

Drinkwater, K. F. 1996. Atmospheric and oceanic variability in the Northwest Atlantic during the 1980s and early 1990s. J. Northw. Atl. Fish. Sci. 18(77-97).

East Coast of North America Strategic Assessment Project; distribution of daubed shanny. 1998. [Online] Available: http://www-orca.nos.noaa.gov/projects/ecnasp/maps/dbshan.gif. (May, 1998).

Ebensperger, L. and Botto-Mahan. 1997. Use of habitat, size of prey and food-niche relationships of two sympatric otters in southernmost Chile. J. Mammal. 78(1): 222-227.

Elliot, R. D., P. C. Ryan and W. Lidster. 1990. The winter diet of Thick-billed Murres in coastal Newfoundland waters. Stud. Avian Biol. 14: 124-139.

Erikstad, K. E. and W. Vader. 1989. Capelin selection by Common and Brunnich's Guillemots during the prelaying season. Ornis Scandinavica 20(2): 151-155.

Nettleship, D. N. and P. G. H. Evans, 1985. Distribution and status of the Atlantic Alcidae. *In* D. N. Nettleship and. T. R. Birkhead, Eds The Atlantic Alcidae. London, Academic Press: 54-154.

Fisher, A. 1988. The Logic of Real Arguments. Cambridge, Cambridge U. Press.

Furness, R. W. and R. T. Barrett. 1985. The food requirements and ecological relationships of a seabird community in North Norway. Ornis Scand. 16: 305-313.

Furness, R. W. and R. T. Barrett. 1990. Ecological responses of seabirds to reductions in fish stocks in North Norway and Shetland. *In* W. Furness and D. N. Nettleship, Eds., International Ornithological Congress 20: Symposium 41; Seabirds as monitors of changing marine environments. R. Wellington, New Zealand. 2246-2256.

Gaston, A. J. and D. N. Nettleship 1981. The Thick-billed Murres of Prince Leopold Island. Ottawa, Canadian Wildlife Service.

Gaston, A. J. 1985a. Development of the young in the Atlantic alcidae. *In* D. N. Nettleship and T. R. Birkhead, Eds. The Atlantic Alcidae. London, Academic Press.

Gaston, A. J. 1985b. The diet of Thick-billed Murre chicks in the eastern Canadian Arctic. Auk 102: 727-734.

Gause, G. F. 1934. The Struggle for Existence. Baltimore, Williams and Wilkins.

Grover, J. and B. Olla. 1983. The Role of Rhinoceros Auklets (*Cerorhinca monacerata*) in mixed species feeding assemblages in the Strait of Juan de Fuca, Washington. Auk 100: 979-982.

Harris, M. P. and S. Wanless 1995. The food consumption of young Common Murres (*Uria aalge*) in the wild. Colonial Waterbirds 18(2): 209-213.

Hatch, S. A. and G. A. Sanger. 1992. Puffins as samplers of juvenile pollock and other forage fish in the Gulf of Alaska. Marine Ecol. Prog. Ser. 80: 1-14.

Hatchwell, B. J. 1991. The feeding ecology and development of young Common Guillemots *Uria aalge* on Skomer Island, Wales. Ibis 133: 153-161.

Hedgren S. and A. Linnman. 1979. Growth of guillemot *Uria aalge* chicks in relation to time of hatching. Ornis Scand. 10: 29-36.

Hobday, D. K. 1992. Abundance and distribution of Pilchard and Australian anchovy as prey species for the Little Penguin *Eudyptulla minor* at Phillip Island, Victoria. Emu 19: 342-354.

Hoffman, W., D. Heinemann and J.A. Wiens. 1981. The ecology of seabird feeding flocks in Alaska. Auk 98: 437-456.

Horn, H. S. 1966. Measurement of "overlap" in comparative ecological studies. Am. Nat. 100: 419-424.

Hunt, G.L., N.M. Harrison and J.F. Piatt. 1992. Diets and selection of foraging habitat by planktivorous auklets in the Bering Sea. *Pac. Seabird Group Symposium.*

Hunt G.L. Jr., A.S. Kitaysky, M.B. Decker, D.E. Dragoo and A.M. Springer. 1996. Changes in the distribution and size of juvenile walleye pollock as indicated by seabird diets at the Pribilof Islands and by bottom trawl surveys in the eastern Bering Sea, 1975 to 1993. NOAA Technical Report.

JWEL, 1997. Marine fauna technical data report. A report submitted to Voisey's Bay Nickel Company by Jaques Whitford Environment Ltd. St. John's Newfoundland.

Lack, D. 1947. Darwin's Finches. Cambridge, University Press.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford: Clarendon Press.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. London: Methuen.

Landres, P. B., J. Verner and J. W. Thomas. 1988. Ecological uses of vertebrate indicator species: a critique. Conservation Biology 2(4): 316-329.

Lawson, J.W., A. Magalhaes and E.H. Miller. 1998. Proximal composition of important prey species for vertebrate predators in the northwest Atlantic. Marine Ecol. Prog. Ser. 164: 13-20.

Levins, R. 1968. Evolution in changing environments. Princeton, NJ, Princeton U. Press.

Lock, A. R., R. G. B. Brown and S.H. Gerriets. 1994. Gazetteer of Marine Birds in Atlantic Canada. Dartmouth, NS, Canadian Wildlife Service.

Lopez, B. H. 1989. Arctic Dreams: imagination and desire in a northern landscape. New York, Bantam.

MacArthur, R. H. 1958. Population ecology of some warblers of northeastern coniferous forests. Ecol 39(4): 599-619.

Magalhaes, A. 1998. Factors affecting proximate composition of prey species important to marine predators in the northwest Atlantic. M.Sc. thesis. Biology. Memorial University of Newfoundland, St. John's, Newfoundland.

Mahoney, S.P. 1979. Breeding biology and behaviour of the Common Murre *(Uria aalge* (pont.)) on Gull Island, NF. M.Sc. thesis. Biology. Memorial University of Newfoundland, St. John's, Newfoundland.

Makushok. 1986. Lumpenidae. *In* P.J.P. Whitehead, M.-L. Bauchot, J.-C. Hureau, J. Nielsen and E. Tortonese Eds: Fishes of the North Eastern Atlantic and the Mediterranean, Vol III. Paris: UNESCO.

Malthus, T. R. 1803. An essay on the principles of population. London, Royal Economic Society.

Mann, K. H. and K. F. Drinkwater. 1994. Environmental influences on fish and shellfish production in the Northwest Atlantic. Environ. Rev. 2: 16-32.

McNamara, J.M., A.I. Houston, and S.L. Lima. 1994. Foraging routines of small birds in winter: a theoretical investigation. J. Avian Biol. 25:287-302.

Miller, D. S. and G. R. Lilly. 1991. Observations and studies on SA2 and Div. 3K Capelin in 1990. CAFSAC Research Document 91(11).

Miller, D. S. 1993. Observations and studies on SA2 and Div. 3K capelin in 1992. DFO Atlantic fisheries research document 93/10.

Monaghan, P., J.D. Uttley and J.D. Okill. 1989. Terns and sandeels: seabirds as indicators of changes in marine fish populations. J. Fish Biol. 35(Supplement A): 339-340.

Monaghan, P., P. Walton, S. Wanless, J.D. Uttley and M.D. Burns. 1994. Effects of prey abundance on the foraging behaviour, diving efficiency and time allocation of breeding Guillemots *Uria aalge*. Ibis 136: 214-222.

Monaghan, P., P. J. Wright, M.C. Bailey, J.D. Uttley, P. Walton and M.D. Burns. 1996. The Influence of changes in food abundance on diving and surface feeding seabirds. *In* W. A. Montevecchi, Ed. Studies of High Latitude Seabirds 4. trophic relationships and energetics of endotherms in cold ocean systems. Ottawa, Canadian Wildlife Service. Occasion Paper 91: 10-19.

Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. Oikos 77: 227-237.

Montevecchi, W. A. and J. F. Piatt. 1984. Composition and energy contents of mature inshore spawning capelin (Mallotus villosus): implications for seabird predators. Comp. Biochem. Physiol. 67A(15-20).

Montevecchi, W. A., V. L. Birt and D.K. Cairns. 1988. Dietary changes of seabirds associated with local fisheries failures. Biol. Oceanogr. 5: 153-161.

Montevecchi, W. A. and A. Berruti. 1991. Avian indication of pelagic fishery conditions in the Southeast and Northwest Atlantic. International Ornithological Congress 20: 2246-2256.

Montevecchi, W. A. and R. A. Myers. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Mar. Ecol. Prog. Ser. 117: 1-9.

Montevecchi, W. A. and R. A. Myers. 1996. Dietary changes of seabirds indicate shifts in pelagic food webs. Sarsia 80: 313-322.

Morisita, M. 1959. Measuring of interspecific association and similarity between communities. Mem. Fac. Sci. Kyushu Univ., Ser. E, Biol. 3: 65-80.

Moser, G.H. and G.W. Boehlert. 1991. Ecology of pelagic larvae and juveniles of the genus *Sebastes*. Env. Biol. of Fishes 30: 203-224.

Murie, D. J. 1995. Comparative feeding ecology of two sympatric rockfish congeners, *Sebastes carinus* (copper rockfish) and *S. malinger* (quillback rockfish). Marine Biology: 342-3353.

NMNH fish collection. 1998. [Online]. Available: http://www.nmnh.si.edu/vert/fishcat/html. (May, 1998).

Ocean Color from Space; global seasonal change. 1998 [Online] Available: http://daac.gsfc.nasa.gov/CAMPAIGN_DOCS/OCDST/ocdst_global_seasonal_change.html. (June, 1998).

Ocean Color from Space; polar productivity. 1998 [Online] Available: http://daac.gsfc.nasa.gov/CAMPAIGN_DOCS/OCDST/ocdst_polar_productivity .html. (June, 1998).

Orians, G.H. 1972. The strategy of the niche. *In* T. B. Allen, Ed. The Marvels of Animal Behavior. Washington, D.C., National Geographic Society.

Parrish, J. K. 1995. Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). Auk 112(2): 390-401.

Pearson, T.H. 1968. The feeding ecology of seabird species breeding on the Farne Islands, Northumberland. J. Anim. Ecol. 37: 521-552.

Pianka. 1981. Competition and niche theory. *In* May, Ed. Theoretical Ecology. MA, Sinaur Assoc.

Piatt, J. F. 1987. Behavioural ecology of Common Murre and Atlantic Puffin predation on capelin: implications for population biology. Ph.D. thesis. Biology. Memorial University of Newfoundland, St. John's, Newfoundland.

Piatt, J. F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. Stud. Avian Biol. 14: 36-51.

Schoener, T. W. 1968. The Anolis lizards: resource use in a complex fauna. Ecol. 49: 704-726.

Schoener, T. W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecol. 51(3): 408-418.

Schoener, T. W. 1974. Resource partitioning in ecological communities. Science 5 July: 27-38.

Schoener, T. W. 1983. Field experiments on interspecific competition. Am. Nat. 122(2): 240-285.

Scripps Institute of Oceanography oceanographic collections. 1997 [Online]. Available: http://gdcmpl.ucsd.edu/sci_coll.html. (May, 1998).

Scott, W.B. and M.G. Scott. 1988. Atlantic Fishes of Canada. Toronto: U. of Toronto Press.

Sergeant, D. E. 1951. Ecological relationships of the guillemots *Uria aalge* and *Uria lomvia*. Poc. X. Int. Ornithol. Congr. 1950: 578-587.

Smith, H. R. and C.L. Remington. 1996. Food specificity in interspecies competition. BioSci. 4(6): 436-447.

Soule, D. F. 1998. Marine organisms as indicators: reality or wishful thinking? *In* D. F. Soule and G. S. Kleppel, Eds. Marine organisms as indicators. New York, Springer-Werlag.

Spring, L. 1971. A comparison of functional and morphological adaptations in the Common Murre (*Uria aalge*) and Thick-billed Murre (*Uria lomvia*). Condor 73: 1-27.

Taber, A. B., A. J. Novaro, N. Neris and F. H. Colman. 1997. The food habits of sympatric jaguar and puma in the Paraguayan chaco. Biotropica 29(2): 204-213.

Tokeshi, M. 1986. Resource utilization, overlap and temporal community dynamics: a null model analysis of an epiphytic chironomid community. J. Anim. Ecol. 55: 491-506.

Trivelpiece, W. Z., S. G. Trivelpiece and N.J. Volman. 1987. Ecological segregation of Adélie, Gentoo and Chinstrap Penguins at King George Island, Antarctica. Ecology 68: 351-361.

Tuck, L. M. 1960. The Murres: their distributions, populations and biology. A study of the genus Uria. Ottawa, Canadian Wildlife Service.

Uttley, J.D., P. Monaghan and S. White. Differential effects of reduced sandeel availability on two sympatrically breeding species of tern. Ornis Scandinavica 20: 273-277.